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Diversity and Adaptation in the Ant Genus *Cephalotes*, Past and Present

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Diversity and Adaptation in the Ant Genus *Cephalotes*, Past and Present (Hymenoptera, Formicidae)

By Maria L. de Andrade & Cesare Baroni Urbani, Basel

With 391 Figures and 7 Tables

"Dum Phaethontea formica vagatur in umbra,
implicuit tenuem sucina gutta feram.
sic modo quae fuerat vita contempta manente,
funeribus facta est nunc pretiosa suis."

"An ant beneath a poplar found,
An amber tear has covered round.
So she that was in life despised,
In death preserved is highly prized"

M. Valerii Martialis Epigrammata VI, 15

Summary

The ant genus *Cephalotes* (= *Zacryptocerus* n. syn. = *Eucryptocerus* n. syn. = *Exocryptocerus* n. syn.) is revised. The following species are described as new in the present paper: Extant species: *argentiventris* (Dominican Republic), *auriger* (Mexico), *betoi* (Brazil), *chacmul* (Mexico), *decolor* (Venezuela), *dentidorsum* (Peru), *ecuadorialis* (Ecuador), *flavigaster* (Dominican Republic), *goniodontus* (Mexico), *guayaki* (Paraguay), *kukulcan* (Belize), *lenca* (Honduras), *mompox* (Colombia), *liepini* (Brazil), *nilpiei* (Brazil), *pallidoides* (Brazil), *pallidus* (Guyana), *palustris* (Guyana), *palta* (Colombia), *pellans* (Paraguay), *persimilis* (Brazil), *persimplex* (Bolivia), *peruviensis* (Peru), *pileini* (Argentina), *resinae* (Dominican copal), *supercilii* (Argentina), *taino* (Dominican copal), *trichophorus* (Peru). Fossil species: *bloosi* (Dominican amber), *brevispineus* (Dominican amber), *caribicus* (Dominican amber), *dieteri* (Dominican amber), *hispaniolicus* (Dominican amber), *maya* (Mexican amber), *olmecus* (Mexican amber), *poinari* (Mexican amber), *sucinus* (Dominican amber), *ventriosus* (Mexican amber).

A completely resolved phylogeny of the genus, based on 131 morphological characters, is tentatively proposed. All the 16 fossil species are extinct today but belong to still existing clades. The Dominican and the Mexican fossils differ from each other at species level but are likely to originate from a homogeneous Mesoamerican fauna. The present study recognizes 131 valid species making *Cephalotes* the largest ant genus confined to the New World.

The evolutionary success of several *Cephalotes* species, demonstrated by their being models of Batesian mimicry for a high number of arthropods, is twofold: a few phylogenetically basal species, like *atratus*, *pusillus*, *minutus*, are geographically widespread and numerically dominant in a variety of environments; other, younger species underwent explosive speciation in the Neotropics. This double success is explained by means of a series of traits peculiar to or uniquely coexisting in *Cephalotes*. The most important of these traits, derived in part from the literature, are presented for the first time in this study. These traits are: 1) frequent polyandry, 2) a diet based largely on a very abundant resource like pollen (this diet is favoured by the pump-filtering action of the proventriculus which reaches, in *Cephalotes*, the highest specialisation known among insects), 3) nesting in pre-existing plant cavities, 4) appearance (among most species) of a separate caste of soldiers devoted essentially to the defence of the nest, 5) a high frequency of spontaneous mutation, 6) a "Bauplan" particularly suitable to passive defence.

Resumo

O gênero de formigas *Cephalotes* (= *Zacryptocerus* n. syn. = *Eucryptocerus* n. syn. = *Exocryptocerus* n. syn.) foi revisado. No presente trabalho são descritas como novas as seguintes espécies Recentes: *argentiventris* (República Dominicana), *auriger* (México), *betoi* (Brasil), *chacmul* (México), *decolor* (Venezuela), *dentidorsum* (Peru), *ecuadorialis* (Equador), *flavigaster* (República Dominicana), *goniodontus* (México), *guayaki* (Paraguai), *kukulcan* (Belize), *lenca* (Honduras), *mompox* (Colômbia), *liepini* (Brasil), *nilpiei* (Brasil), *pallidoides* (Brasil), *pallidus* (Guiana), *palustris* (Guiana), *palta* (Colômbia), *pellans* (Paraguai), *persimilis* (Brasil), *persimplex* (Bolívia), *peruviensis* (Peru), *pileini* (Argentina), *resinae* (copal dominicano), *supercilii* (Argentina), *taino* (copal dominicano), *trichophorus* (Peru). Espécies fósseis: *bloosi* (âmbar dominicano), *brevispineus* (âmbar dominicano), *caribicus* (âmbar dominicano), *dieteri* (âmbar dominicano), *hispaniolicus* (âmbar dominicano), *maya* (âmbar mexicano), *olmecus* (âmbar mexicano), *poinari* (âmbar mexicano), *sucinus* (âmbar dominicano), *ventriosus* (âmbar mexicano).

Uma filogenia completa das espécies do gênero baseada em 131 caracteres morfológicos é proposta. Todas as espécies fósseis são hoje extintas, mas pertencem a grupos de espécies Recentes. Os fósseis dominicanos e mexicanos diferem entre si a nível específico mas provavelmente originaram-se de uma fauna Mesoamericana homogênea. O presente estudo reconhece 131 espécies válidas tornando *Cephalotes* o maior gênero de formigas endêmico do Novo Mundo.

O sucesso evolutivo de muitas espécies de *Cephalotes*, demonstrado pelo fato que suas espécies são modelos frequentes de mimestismo Batesiano para muitos artrópodos, é duplicado: algumas espécies dos grupos basais, como *atratus*, *pusillus*, *minutus*, tem uma ampla distribuição geografica e são numericamente dominantes em vários ambientes; outras espécies dos ramos apicais sofreram uma especiação explosiva na Região Neotropical. Esse duplo sucesso é explicado por meio de uma série de caracteres peculiares de ou unicamente coexistentes em *Cephalotes*. Dentre estes caracteres os mais importantes, parcialmente retirados da literatura, são discutidos pela primeira vez neste estudo: 1) poliandria frequente, 2) uma dieta largamente baseada em uma fonte abundante como pólen (esta dieta é favorecida pela ação da bomba-filtro do proventrículo a qual alcança, em *Cephalotes*, a maior especialização conhecida entre os insetos), 3) nidificação em cavidades pré-existentes de plantas, 4) aparecimento (na maioria das espécies) de uma casta separada de soldados destinados essencialmente à defesa do ninho, 5) uma alta frequência de mutação expontânea e, 6) um "Bauplan" particularmente adaptado à defesa passiva.

Zusammenfassung

Die Ameisengattung *Cephalotes* (= *Zacryptocerus* n. syn. = *Eucryptocerus* n. syn. = *Exocryptocerus* n. syn.) ist Gegenstand vorliegender Revision. Folgende Arten werden in der vorliegenden Arbeit neu beschrieben: Rezente Arten: *argentiventris* (Dominikanische Republik), *auriger* (Mexico), *betoi* (Brasilien), *chacmul* (Mexico), *decolor* (Venezuela), *dentidorsum* (Peru), *ecuadorialis* (Ecuador), *flavigaster* (Dominikanische Republik), *goniodontus* (Mexico), *guayaki* (Paraguay), *kukulcan* (Belize), *lenca* (Honduras), *mompox* (Kolumbien), *liepini* (Brasilien), *nilpiei* (Brasilien), *pallidoides* (Brasilien), *pallidus* (Guyana), *palustris* (Guyana), *palta* (Kolumbien), *pellans* (Paraguay), *persimilis* (Brasilien), *persimplex* (Bolivien), *peruviensis* (Peru), *pileini* (Argentinien), *resinae* (Dominikanischer Kopal), *supercilii* (Argentinien), *taino* (Dominikanischer Kopal), *trichophorus* (Peru). Fossile Arten: *bloosi* (Dominikanischer Bernstein), *brevispineus* (Dominikanischer Bernstein), *caribicus* (Dominikanischer Bernstein), *dieteri* (Dominikanischer Bernstein), *hispaniolicus* (Dominikanischer Bernstein), *maya* (Mexikanischer Bernstein), *olmecus* (Mexikanischer Bernstein), *poinari* (Mexikanischer Bernstein), *sucinus* (Dominikanischer Bernstein), *ventriosus* (Mexikanischer Bernstein).

Basierend auf 131 morphologischen Merkmalen wird eine vollständige Phylogenie vorgeschlagen. Alle fossilen Arten sind heute ausgestorben; sie gehören aber noch immer rezenten Gruppen an. Dominikanische und mexikanische Fossilfunde unterscheiden sich auf dem Artniveau, ihr Ursprung dürfte jedoch eine homogene mesoamerikanische Fauna gewesen sein. Die vorliegende Studie beschreibt 131 gültige Arten; damit ist *Cephalotes* die artenreichste Ameisengattung exklusiv der Neuen Welt.

Innerhalb der Gattung *Cephalotes* findet man Beispiele besonderen evolutionären Erfolgs. Das zeigt sich schon daran, daß bestimmte Arten von zahlreichen Arthropoden imitiert werden (Bates'sche Mimikry). Außerdem haben einige phylogenetisch ältere Arten, wie *atratus*, *pusillus* und *minutus*, eine weite geographische Verbreitung und sind in bestimmten Biotopen dominant. Andere, phylogenetisch jüngere Arten wiederum erfuhren in der Neotropis explosionsartige Speziationen. Beide Aspekte werden mit einer Reihe von Merkmalen erklärt, welche der Gattung *Cephalotes* eigen sind oder gar nur bei dieser zusammen vorkommen. Die wichtigsten Merkmale hierzu sind teilweise der Literatur entnommen, teilweise werden sie aber in der vorliegenden Arbeit zum ersten Mal beschrieben. Im Einzelnen sind dies: 1) häufige Polyandrie, 2) Ernährung, die auf reichlich vorkommender Nahrung, sprich Pollen, basiert (stark begünstigt wird diese Ernährungsweise durch einen Pump- und Filter-Mechanismus des Kaumagens, welcher bei *Cephalotes* den höchsten Spezialisationsgrad unter den Insekten erreicht), 3) Anlegen von Nestern in bestehenden Hohlräumen von Pflanzen, 4) Erscheinen einer separaten Soldatenkaste (bei den meisten Arten), welche im wesentlichen Aufgaben der Nestverteidigung übernimmt, 5) häufig auftretende, spontane Mutationen, 6) ein "Bauplan", welcher sich besonders gut zur passiven Verteidigung eignet.

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1. Introduction

Cephalotes is the type genus of a tribe of very characteristic myrmicine ants (Cephalotini) essentially confined to the Neotropical region and reaching the Nearctic only in southern parts of Florida, Texas and Arizona.

The grotesque morphology of the Cephalotini fascinated a variety of people of different epochs and of different cultures (see also FRANZ, 1942).

The first published record of S. American ants probably refers to the largest and commonest species of the tribe (*Cephalotes atratus*) since, according to DE DALLA TORRE (1893), the "*Formica... mufcæ majori æqualis*" described by the official naturalist of the governor-general of Dutch Brazil (MARCGRAVIUS DE LIEBSTAD, 1648) should be identified with it. SMITH (1854) first outlined the uniqueness of these ants writing that "there is no genus with which we are acquainted amongst the *Formicidae* which exhibits such eccentricities of form". DARWIN (1859) epitomised the mor-

phology and caste system of Cephalotini in the following terms: "the workers of one caste alone carry a wonderful sort of shield on their heads". FARREN WHITE (1895) was so impressed by the bizarre cephalotine look that he wrote: "Some ants are most eccentric in their general appearance. I have noticed one carrying on its head what looked exactly like a tea-tray of old-fashioned shape". SHARP (1899) considers that "these ants assume a great variety of shapes and forms, some of which look almost as if they were the results of an extravagant imagination". RUZSKY (1905) states that they have "очень характерныя формы... [и] строеніе вообще головы и торакса своеобразно" (very characteristic forms... [and] the structure of the head and thorax is peculiar). WHEELER (1910) alludes to them as having "wonderful heads", a morphological trait stressed again by EMERY (1915 b) who writes that they possess "soldati col capo di figura stravagante, atto a fare da tappo alla porta del nido". BRUN (1924) considers the Cephalotini as "auffallend plattgedrückt" and FOREL (1925) refers to the same morphology by adding that "ce singulier phénomène... attend aussi son interprétation par une étude attentive des moeurs". EIDMANN (1936) conceives *C. atratus* as a "wundervolle, große und auffallende Ameise". BERNARD (1951) reiterates the judgement of SMITH (1854) stating that the Cephalotini, among ants, are "les plus curieux d'aspect". GOETSCH (1953) also focuses the general body shape of these ants which he defines as "unglaublich... ganz breiten, plumpen, verhältnismäßig kurzbeinigen Arten".

Fig. 1. Aerial view of one of the lines of Nasca (Peru) representing abstract animal contours (left) and the contour of a worker of *Cephalotes atratus* (LINNAEUS) drawn in the same style (right). The Nasca design was interpreted as a spider, essentially because it has four pairs of legs. We contend that the Nasca design might refer to a cephalotine ant as well. The reasons for this claim are twofold: (1) cephalotines are much more common and impressive than spiders, and, (2) the Nasca design bears a typical insect character contradicting the spider interpretation, namely the separation between head and thorax. This latter character is considered as being of easier observation than the number of appendages.

In Brazil at least two species of Cephalotini have vernacular names: *Zacryptocerus pusillus* is called "cascuda" (the one with thick skin), and *Cephalotes atratus* bears the Indian names of "tarapé" or "tarapema" (literally, which has spines on the back) (SANTOS, 1985). In Venezuela JAFFE & MULLER (1979) report that the Ye'cuana Indians have names for 38 different ants, two of which are Cephalotini: one is *Cephalotes atratus* (yakë tamuru) and the other are members of the genus *Zacryptocerus* (ahaadi). In a similar manner, the Yanomami Indians know 39 ant names two of which are Cephalotini: *Zacryptocerus clypeatus* (he resina) and *Cephalotes atratus* (hupewe or huperiwe) (HERZOG et al., 1979).

We think that records of Cephalotini may be found also in pre-Columbian cultures and we like to believe that one of the famous Peruvian designs of Nasca traditionally interpreted as a spider could actually represent a cephalotine ant (Fig. 1). The spider interpretation is based on a very good character indeed: the Nasca drawing depicts an animal with four pairs of legs instead of three. As a matter of fact, this excellent zoological argument is ordinarily ignored by non-zoologists. On the other hand, the drawing possess an easily observable insect character contrasting with the spider interpretation: the head separate from the mesosoma. In addition to the above "morphological" argument, we can add an ecological one: Cephalotini are much more frequent, easier to observe, and more impressive for their behaviour and social life, than are spiders. The fact that there are species of spiders imitating the body shape of the Cephalotini (see Chapter 6.6) and not the contrary can be considered as an indirect proof of our claim. We do not intend to categorically repudiate all previous published explanations of this Nasca drawing and we concede that our fascination for the Cephalotini may have biased our speculation, but we assert that the new interpretation we suggest is as credible as the former one.

The relationships of the Cephalotini with other myrmicine tribes are far from being clear. The oldest literature contains intuitive suggestions about their possibly closest ant taxa as being the Old World tribe Myrmecinini (EMERY, 1920, 1922) or the largely Old World genus *Tetramorium* (FOREL, 1892). The relationship with the Myrmecinini was probably inferred from the fact that all Cephalotini share with the genus *Myrmecina* (but not with other genera of the tribe) a sessile petiole and a hard integument.

The reasons for this uncertainty lie in the fact that the general habitus of the Cephalotini is matchless among all the Formicidae and presents in this way very distinctive characters which are likely to be uniquely derived for the tribe but offer very little potential synapomorphies with other ant clades.

On the basis of their morphological peculiarities LATREILLE (1802 b) separated the Cephalotini in a distinct "family" of ants, "les Fourmis chaperonnées" or "*Formicae caperatae*", a name probably referring to the frontal carinae covering the antennae. And the same arguments explain why the type genus of the tribe, *Cephalotes* (κεφᾱλωτός in Greek means headed), is the second ant genus ever named (by LATREILLE, 1802 a), the first being, of course, the Linnean *Formica*.

A similar course of action was undertaken by SMITH (1867) who created the "Cryptoceridae" as a new subfamily of Formicidae destined to include all known Cephalotini plus *Cataulacus* and *Meranoplus*. This classificatory scheme has been shown to be inconsistent by EMERY (1893).

More than one hundred years after Latreille, on the basis of similar considerations, a famous, controversial paper by ASHMEAD (1905) again considered the Cepha-

lotini as being separate from (most of) the remaining Formicidae and constituting (the main part of) one of the seven distinct families into which he divided the superfamily Formicoidea. ASHMEAD's classification, as a matter of fact, was promptly and severely criticised by EMERY (1906) and the tribal rank of the Cephalotini within the Myrmicinae has remained unchanged since that date.

The position of FOREL (1917), however, differs from the previous ones essentially with respect to the rank he accorded to the Cephalotini. In fact he introduced a new "section" within the subfamily Myrmicinae, the Rhagomyrmicinae, destined to include again the Cephalotini, the Cataulacini and the Dacetonini. The similarity with the subfamily Cryptoceridae created by SMITH (1867) did not escape EMERY (1921) who rejected this section on the same (intuitive) phylogenetic arguments he used to reject the Cryptoceridae.

Among the most unusual synapomorphies of the tribe one should mention at least the bizarre mushroom-shaped morphology of the proventriculus, an important character already described by FOREL (1878). As we already said, this and other morphological traits leave little doubt as to whether the Cephalotini should be regarded as a separate tribe, but do not help in clarifying their relationships with other ants. In the Old World fauna, the monotypic tribe Cataulacini shares with the Cephalotini 11-jointed antennae in all female castes as well as a similar cephalic morphology, although the frontal carinae of *Cataulacus* are below the eyes instead of over the eyes as in the Cephalotini. In his tentative phylogeny of the myrmicines EMERY (1914 a) attributed to both tribes a close, unprecised position between his "Myrmecinini primitivi" and the highly specialised Attini and Dacetonini. It is on the basis of similar considerations that FOREL (1917) grouped the two tribes (and others as well) under the name Rhagomyrmicinae but his point of view was contradicted by EMERY (1921: 2) who considered the similarities between the two groups as superficial and due to convergence. Curiously enough, the phylogeny of page 8 of the same EMERY (1922) monograph in which close phylogenetic relationships between Cephalotini and Cataulacini are denied, repeats his former (1914 a) diagram in which the Cephalotini and Cataulacini are drawn close to each other, though with unknown origins. This latter point of view has been the dominant one in the ant literature until recently (see also BOLTON, 1974).

The convergence hypothesis between the Cephalotini and the Cataulacini has never been wholly justified but it was presumably derived from the strict geographic vicariance of the two tribes (Fig. 2). Vicariance, however, is in perfect agreement with the hypothesis of allopatric speciation of two clades originated from a unique ancestor. It is clear that if the (still undemonstrated) close phylogenetic relationship between the two tribes could be proven, the appearance of the same characters in both tribes by parallelism or by convergence instead of by inheritance through common ancestry would be improbable.

The parallelism/convergence hypothesis was particularly supported by BEQUAERT (1922 b) and KUSNEZOV (1963) who re-asserted the non relatedness of the two groups (without justifying it) and explained the morphological similarities by the similarity in behaviour. The same opinion has been better documented by WHEELER & WHEELER (1954 b). These authors described similarities between the two tribes in larval morphology and justified the convergence hypothesis by stressing how these same characters can be found in a number of genera belonging to different subfamilies sharing an important ecological trait: nesting in plant cavities. On

the other hand, the larvae of the two tribes can be separated only by the morphology of their dorsal hairs: single-hooked in the Cataulacini and double-hooked in the Cephalotini. Both hair morphologies, however, are found equally in a wide array of non related genera. More recent detailed studies on the comparative morphology of the sting apparatus (KUGLER 1978 & 1979) suggest non-adaptive similarities between the two tribes. In particular, the sting of *Procryptocerus* (Cephalotini) – with dorsally reduced sting shaft – is more similar to that of *Cataulacus* than to that of other Cephalotini (see e. g. KUGLER, 1979, Fig. 5). Another structure, believed to be present in, and unique to, all the Cephalotini genera, i. e. a thick ileum filled with microscopic fungi and bacteria (CAETANO & DA CRUZ LANDIM, 1987), has been recently described in *Cataulacus* as well (CAETANO et al., 1994).

The primary motivation for the present work was our chance to examine a collection of 130 fossil Cephalotini from different museums and private collections, 125 in Dominican amber and 5 in Mexican amber. To give an idea of the importance of this material for the palaeontology of ants, when we started our project the literature contained numerous superficial references to Dominican amber Cephalotini but not a single fossil species had been identified. Moreover, in spite of their eccentric morphology attracting a variety of observers with different interests, no fossil Cephalotini had been reported from anywhere else in the world. We were particularly excited about the Mexican amber specimens: the current information on the Mexican amber ant fauna is limited to one species described on only one specimen (DE ANDRADE, 1995).

If, on one hand, it took us only a few days to understand that our amber Cephalotini should be assigned to over a dozen different species, all undescribed, we faced continuous, great difficulties in establishing even approximate relationships among

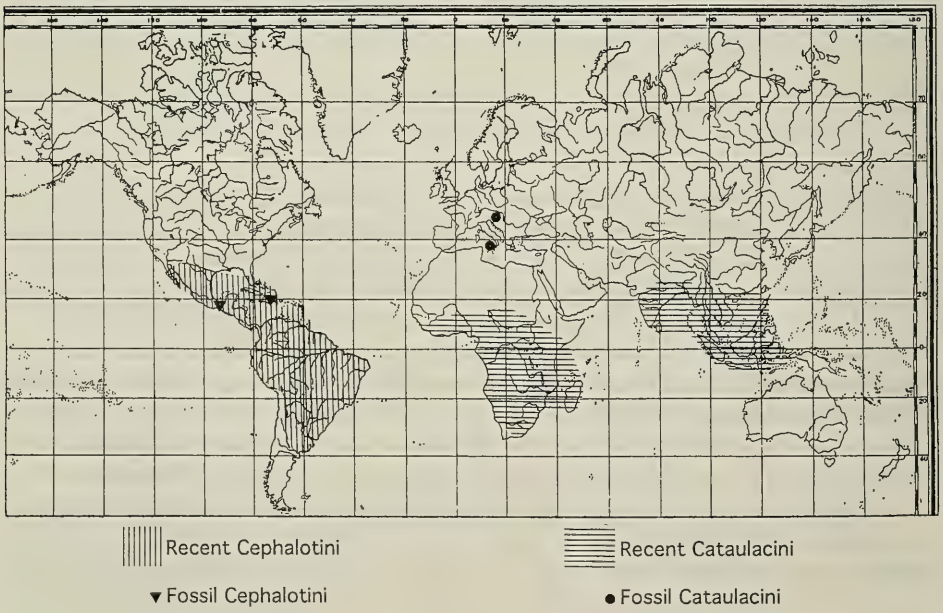


Fig. 2. Distribution of the ant tribes Cephalotini and of the morphologically similar, geographically vicariant Cataulacini.

them and with the known Recent species. Moreover, some of the most striking morphologies of these ants and the unique caste system of *Zacryptocerus* were already present, sometimes in exaggerated form, in the fossil record.

In the attempt to understand as much as possible of the cephalotine diversity, past and present, we felt compelled to deal with different aspects of the biology of these ants including in our analysis Recent and fossil species together.

During the present study, in addition to the fossil material, we have been able to examine fresh Cephalotini material from several countries, and a few specimens from Dominican copal. Our primary task was to infer the most probable phylogenetic relationships between the fossil and the Recent species; the ultimate task was to gather sufficient information on these ants to explain at least some of their numerous, easily observable, peculiar traits.

1.1. Previous records of fossil Cephalotini

Fossil Cephalotini are not uncommon in Dominican amber and, due to their grotesque morphology, there are quite a few reports of their occurrence. In this paper we shall describe all Dominican species known so far and the first records from Mexican amber. No true or presumed fossils of this tribe have ever been reported from other localities, including the rich and well known ant faunas of the Baltic amber (WHEELER, 1915) and of the Florissant shales (CARPENTER, 1930). The published mentions of fossil Cephalotini known to us are the following:

BARONI URBANI & SAUNDERS (1982) give photographs of one specimen and drawings of two species cited as undescribed *Zacryptocerus*; SCHLEE (1980) published a colour photograph of *Zacryptocerus* sp. (representing the same species as the one drawn in Plate III, Fig. 1 by BARONI URBANI & SAUNDERS, l. c.); WILSON (1985 a, b) records the presence in Dominican amber of *Paracryptocerus* (re-raising in this way to generic rank a name synonymised with *Zacryptocerus* by KEMPF, 1973); POINAR (1992) shows drawings of two *Paracryptocerus* specimens apparently belonging to only one species and a photograph of a third specimen probably referring to the same species already illustrated by SCHLEE (l. c.) and by BARONI URBANI & SAUNDERS (l. c.). One of the drawings published by BARONI URBANI & SAUNDERS (1982, Plate II, Fig. 2) has been reproduced by JASTRZEBSKI (1985: 1) and on the front cover of a publication of the "Museum für Gestaltung" in Zurich (ANONYMOUS, 1990). WAGENSBERG (1995) published a colour picture of an unidentified Cephalotini in Dominican amber. This same picture, enlarged, has been reproduced as a poster and published in a newspaper (ANONYMOUS, 1995) and has been published again by WAGENSBERG & SERRANO (1997).

The recent work by VIERBERGEN & SCHEVEN (1995) deserves special mention. Since we might, in a sense, bear some responsibility for this paper, we are willing to explain its antecedents here at some length. On December 27, 1991 Mr. Vierbergen wrote to Baroni Urbani asking for advice about his project to study amber *Zacryptocerus*. Baroni Urbani replied that he had a student (de Andrade) beginning to work on the same ants and, as a demonstration of this, he enclosed in his letter drawings of four undescribed amber *Zacryptocerus* (two of which already published by BARONI URBANI & SAUNDERS, 1982). Mr. Vierbergen replied sending some of his drawings and adding that he would like to cooperate with de Andrade. We discussed the proposal and, considering the quality of the drawings, the geographic distance, and the lack of information on the scientific background of Mr. Vierbergen, we decided to

ignore it. It was only in 1995 that, during a visit to the Museum of Comparative Zoology in Harvard, de Andrade saw some amber specimens identified by Mr. Vierbergen and bearing very questionable generic and specific identifications. Baroni Urbani, in September, wrote Mr. Vierbergen listing the erroneous interpretations detected by de Andrade and urging him not to publish them. Mr. Vierbergen replied that he did not realise that our intention was to work on these ants and that his paper was already in press and due to appear by the end of the year. And, in January 1996, we received a photocopy of it.

This paper, in some respects, was beyond our expectations. The article dealt only with three of the four species of which we sent drawings: one of them was described three times as three new species in a new genus, etc. The strictly taxonomic or entomological merits of this work will be discussed at the proper places in our treatment of the fossil Cephalotini, but the paper (published by the Creation Research Society) attracted our attention for other reasons which we shall not have the opportunity of mentioning elsewhere.

The main conclusion from the study of amber Cephalotini is "a depauperation... of the ant fauna... before or shortly after the Flood". We agree. The statement "before or shortly after the Flood" is comprehensive enough as to be true under any conceivable circumstance. It does not, however, represent a proof of the Flood. On the contrary, it focuses on the insignificant biogeographic relevance of the Flood.

The discussion and the conclusions are completed by a note in which the Editor of the journal stresses the interest of amber ants "supposed to have fossilised millions of years ago" and which "cannot be used to formulate theories on macroevolution!". We agree only in part. From our studies on Miocene Cephalotini we drew not theories but firm conclusions about the dramatic local extinctions and explosive speciation events which occurred in the Caribic fauna after amber times, we established a minimum age for the evolution of the extraordinary caste system of *Cephalotes* and we improved our understanding of the phylogeny of the Recent species. On the other hand, if the macroevolutionary theories alluded to are customary subjects like the origin of birds or the extinction of dinosaurs, we must concede to the Editor of the Creation Research Society Quarterly that our best efforts at understanding the evolution of *Cephalotes* during the last 15 – 40 million years have proven insufficient to add a single inference on these topics.

Since the available literature we mentioned above made use of three different generic names to deal with a set of very similar ants, we have been compelled to detail the exact generic attribution of the specimens we studied as well as the most plausible limits for the recognisable Cephalotini genera.

2. Material examined

The initial aim of the present paper was to offer detailed descriptions of the fossil Cephalotini to be compared with the extant species of the tribe. The sources of fossil Cephalotini available to us are the following collections reported here with their respective codens as given by Arnett & Samuelson (1986), when available, or with new ones written by us for the present study, when necessary:

SMNS. Staatliches Museum für Naturkunde in Stuttgart (courtesy of Dr. Dieter Schlee).

GOPC. Collection George O. Poinar, deposited at the Oregon State University, Corvallis, Oregon (courtesy of Dr. George O. Poinar, Jr.).

JSHC. Collection Joachim Scheven, Hagen, Germany (courtesy of Dr. Joachim Scheven).

MCCB. Museu de la Ciència, Fundació "la Caixa", Barcelona (courtesy of Prof. Jorge Wagensberg).

MCZC. Museum of Comparative Zoology, Harvard University, Cambridge, Mass. (courtesy of Mr. Stefan Cover).

NHMB. Naturhistorisches Museum in Basle (courtesy of Dr. M. Brancucci).

The great majority of the Cephalotini specimens in amber have the entire body or large portions of it covered by a tiny gaseous film producing silver reflections under strong direct illumination. Not only does this film not prevent examination of the specimens, but it sometimes makes the appreciation of microsculptural details easier. Unless otherwise stated under the specimen's preservation conditions given below, each specimen is covered by a gaseous film at least to a major extent. We consider it useful to give a superficial description of the amber (or copal) sample in which the ants are included, of the presence in it of other organic inclusions, and of the size of the amber sample. We made no efforts, however, to identify the other inclusions in an exact way and the measurements of the amber sample are always given as maximum length and maximum width of the sample as positioned without support. The following fossil and subfossil specimens of Cephalotini were available for the present study:

From the SMNS

Dominican amber

Do-181. An oval 1.4x1.0 cm dark yellow amber piece containing several air bubbles and a fissure, and an ant worker close to the surface with the dorsal and left lateral sides which result, in this way, the sole well observable sides.

Do-277-K. An intact worker perfectly observable, embedded in a small piece of yellow amber of 1.0x0.8 cm.

Do-333-K. An intact worker perfectly observable, embedded in a small piece (0.7x0.5 cm) of dark yellow amber (Fig. 3).

Do-506. A brown 3.5x2.5 cm amber sample with an intact worker. The head is partly covered by a small air bubble and by a transversal fissure in amber. Otherwise perfectly visible (Fig. 7 C).

Do-551. Light yellow amber (2.6x1.7 cm) containing a worker with the postpetiole asymmetrically deformed; the right gena and the tip of right antenna superficially destroyed by polishing. An air bubble on the right side of the propodeum and a fissure parallel to the sagittal plane on the left ant side. Otherwise well observable specimen in dorsal view.

Do-618-K. A small amber piece (0.7x0.4 cm) containing a single worker. The amber bears several small air bubbles preventing examination only to a minor extent (Fig. 16 A).

Do-974-K. Light, small amber piece (0.8x0.8 cm) with an intact worker perfectly observable; only part of the head, the right humerus and part of the gaster covered by gaseous film.

Do-1069-K. A piece of light yellow amber containing a small leaf, several small impurities and two worker ants cut and polished separately as follows: Do-1069-K-1, 1.6x1.2 cm, intact specimen, postpetiole and first gastral segment slightly deformed, ventral and lateral views practically impossible due to the amber inclusions and impurities, dorsal view good (Fig. 5 C); Do-1069-K-2, 1.5x0.6 cm specimen lacking the terminal gastral segments, very good dorsal view of the head and of the mesosoma (Fig. 4 A & C).

Do-1898. Large (3.5x2.0 cm) piece of yellow amber from which the ant worker has been separately cut and polished; the specimen is largely but not entirely covered by a gaseous film, both metatarsi and part of the left metatibia are missing, otherwise a specimen perfectly observable from every side.

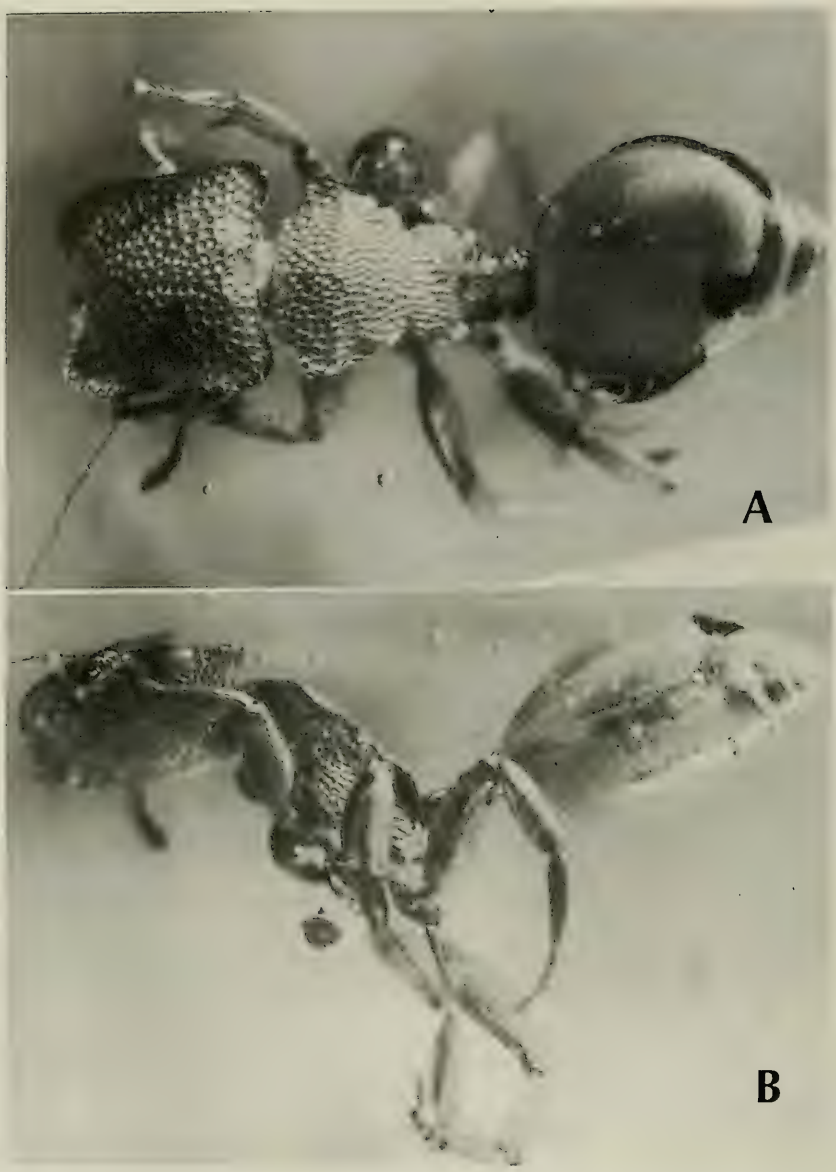


Fig. 3. Dominican amber. Specimen Do-333-K. – A: Dorsal view. – B: Lateral view.

Do-1978. A piece of yellow amber (1.5x1.5 cm) containing many small soil particles and a worker ant with the first gastral tergite slightly confused; right funiculus, right mid tarsomeres and right hind tarsus missing.

Do-1980. Large (3.0x1.2 cm) piece of yellow amber cut straight and polished dorsally to the ant worker which is partly shaded by an air bubble on the left side (Fig. 7 A).

Do-2001. A piece (3.0x1.7 cm) of partly rough, dark yellow amber cut transversally and polished to study the single ant worker included in it; good dorsal and right lateral vision.

Do-2043. Round (Ø 1.4 cm) yellow amber piece with the ant worker close to the surface; half of the gaster, left metafemur, meso- and metatibia and meso- and metatarsus missing.

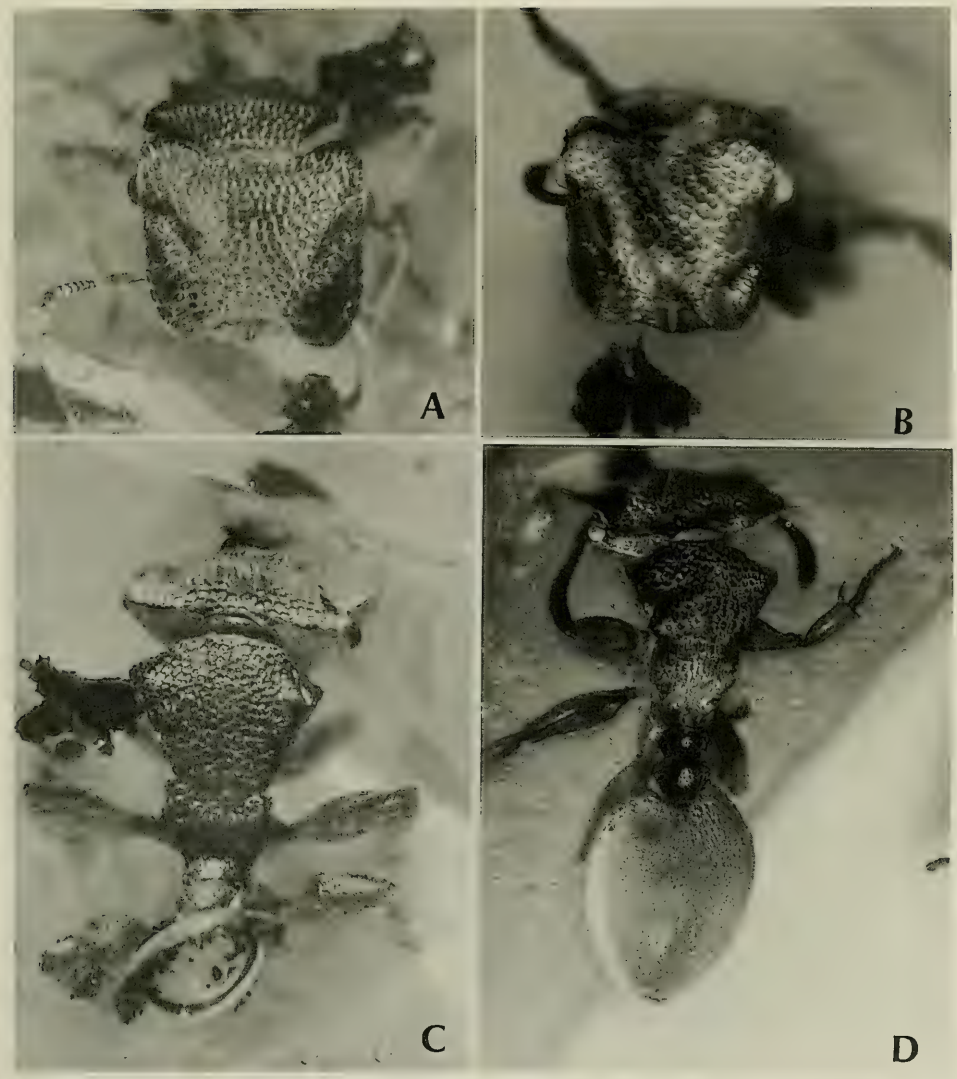


Fig. 4. Dominican amber. Specimen Do-1069-K-2. – A: Full frontal view of the head. – C: Dorsal view. Specimen Do-3487. – B: Full frontal view of the head. – D: Dorsal view.

Do-2455. A dark yellow 2.0x1.5 cm amber piece with the ant body affected by a dorsal longitudinal crack almost on the sagittal plane not affecting examination of the specimen (Fig. 8 B).

Do-2457. Light yellow, oval amber specimen 2.5x1.9 cm containing a termite, an *Azteca* worker, and the cephalotine ant without gaster and obscured by a major fissure; difficult examination essentially of the head in frontal and ventral view.

Do-2622. Light yellow amber piece with several leaf fragments and cracks. The ant specimen with the gaseous film on the mesosoma only. Reasonable dorsal and left lateral vision.

Do-2700. Oval 1.6x1.2 cm orange amber piece cut longitudinally to enable the study of the ant specimen. The ant body is covered by the gas layer only on the gaster and on the occipital angles; right posterior leg missing; excellent vision from every side.

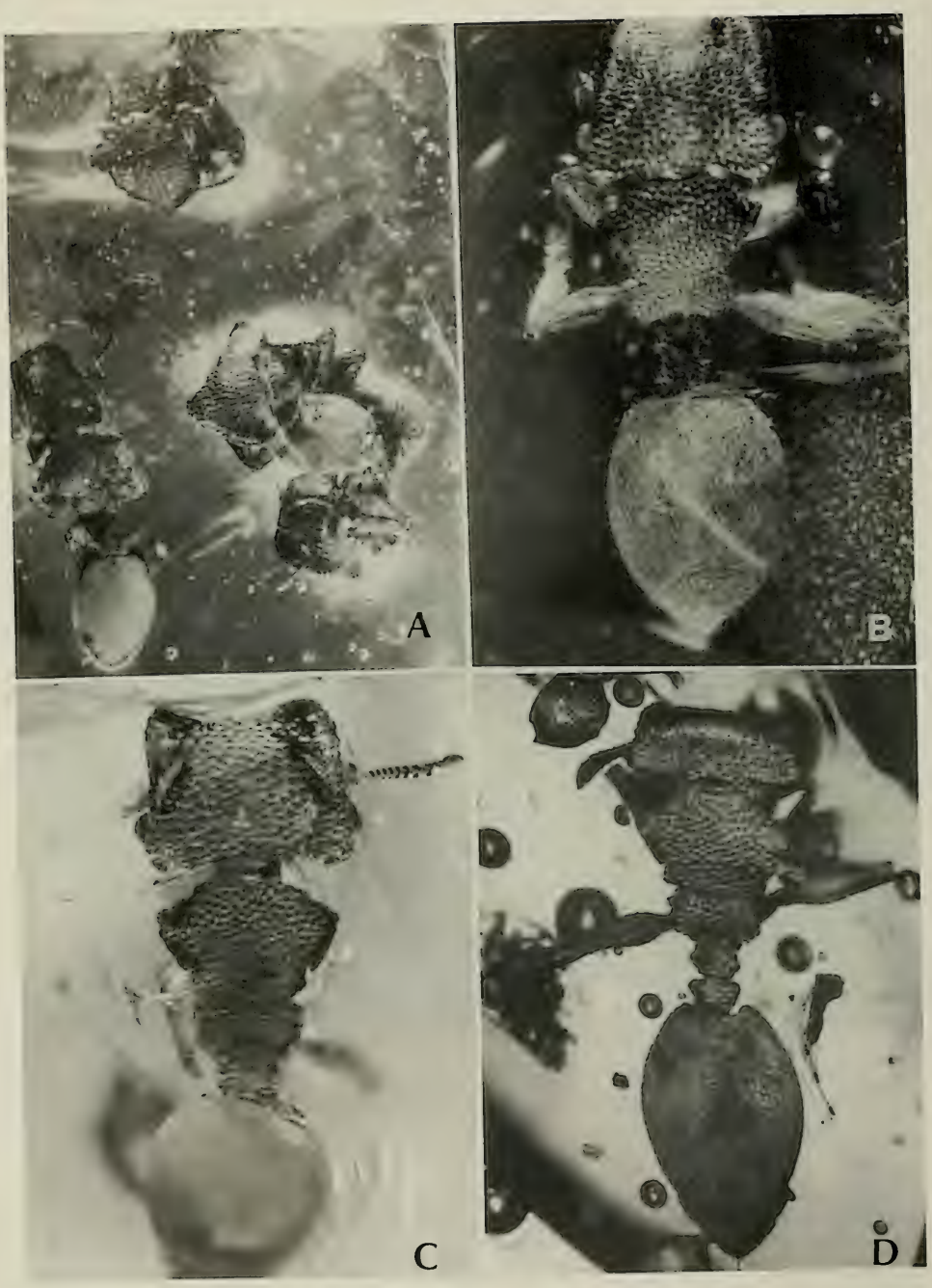


Fig. 5. Dominican amber. – A: Amber sample Do-4210 including four Cephalotini workers. – B: Specimen Do-4480, dorsal view. – C: Specimen Do-1069-K-1, dorsal view. – D: Specimen Do-5163, dorsal view.

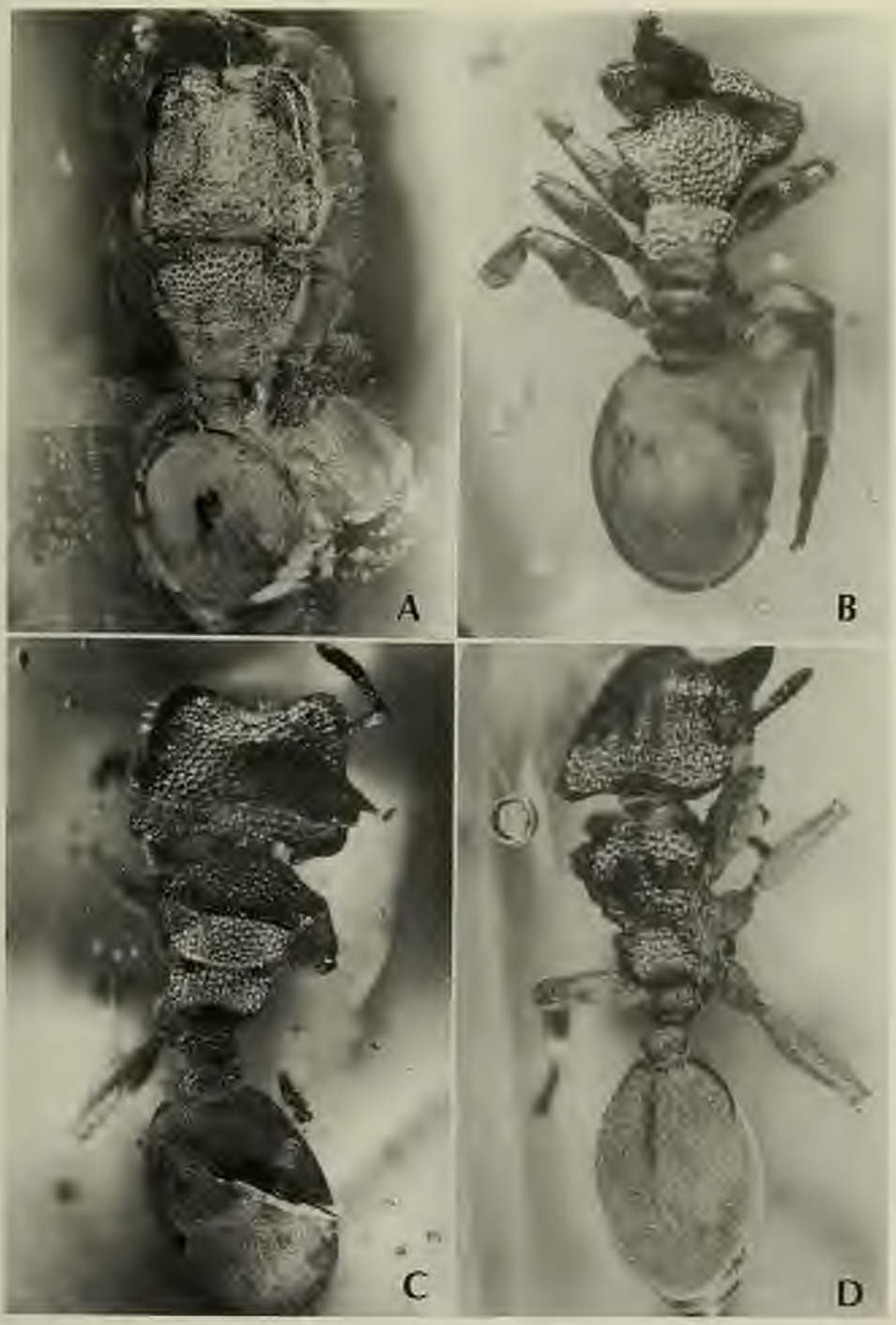


Fig. 6. Dominican amber. – A: Specimen Do-5492, dorsal view. – B: Specimen H 10-116 D, dorsal view. – C: Specimen H 10-116 B, dorsal view. – D: Specimen H 10-116 E, dorsal view.

Do-2759. Oval 2.0x0.9 cm light yellow amber piece successively cut to improve vision. The ant lacks the right pro- and mesotarsi; examination of the specimen is rendered difficult by the presence of several small longitudinal and transverse cracks.

Do-2806. 2.4x1.1 cm dark amber piece re-cut to improve examination of the ant. The body of the specimen is crossed by several adjacent cracks and air layers. Limited vision in dorsal view restricted to the head, the prothorax, most of the pedicel, and the gaster.

Do-2807. 2.2x1.5 cm sample of orange amber successively cut and re-polished to improve vision. The ant, embedded in amber in the stereotyped defence position with the gaster raised upwards is well observable from every side.

Do-3128. A dark yellow amber piece (1.9x2.6 cm) with included a winged termite, a microhymenopteron, a *Pseudomyrmex* worker without head, and the cephalotine ant. The latter is intact and close to the surface enough as to enable good examination from every side.

Do-3224. Oval, 2.0x1.2 cm, yellow amber sample successively cut and re-polished to improve the study of the ant. The ant appears complete but strongly compressed dorsoventrally; minute impurities around the body reduce the vision.

Do-3274. Large (3.7x2.0 cm) dark yellow amber piece successively cut and re-polished to improve vision of the inclusions; these comprise a spider, a badly deformed *Azteca* worker, several impurities and the cephalotine worker; the latter appears strongly compressed dorsoventrally and shaded on part of the right side by an air bubble; by contrast, the body is free from the gaseous film and the resulting bicolour body is well visible.

Do-3316. Elongate (4.7x2.0 cm), brown amber sample successively cut and re-polished. The inclusions are insect excrement, several small air bubbles, a microhymenopteron, a *Pseudomyrmex* gyne without head, and the cephalotine ant. This is intact and, in spite of the presence of some air bubbles and a possible seed fragment close to the body, dorsal and lateral visibility is good (Fig. 10 A).

Do-3326. 1.5x1.2 cm dark yellow amber sample successively cut and re-polished. Besides the ant a tipulid is included. The ant is intact but affected by some minor cracks and air bubbles; frontal, dorsal, and right lateral vision good (Fig. 12 C).

Do-3487. Yellow amber sample 1.9x1.5 cm. Included are a spider exuvia and the ant which has been separated and re-polished for the present study. The ant lacks the right meso- and metatarsi. The gaseous film around the body does not cover the abdominal pedicel and the appendages giving the wrong impression of a bicoloured species. Otherwise a perfectly visible specimen (Fig. 4 B & D).

Do-3581. 2.0x1.7 cm yellow sample including only the ant, a few vegetable fragments, and insect excrement. The ant has been separated and re-polished for the present study. In spite of two small air bubbles, one close to the abdominal pedicel and another under the head it is very clearly visible (Fig. 9 C & D).

Do-3765. 3.0x1.4 cm yellow sample affected by several cracks. The ant is intersected by a minor longitudinal crack and by a major horizontal fissure over the gaster. Dorsal vision of the head, mesosoma and pedicel satisfactory.

Do-3792. Dark yellow but very clean 3.5x1.8 cm sample containing, besides the ant, 9 diptera, a coleopteron and other insect fragments. The ant is intact but close to a (?) limoniid dipteron not disturbing the dorsal vision (Fig. 12 A).

Do-3817. 1.3x1.0 cm dark yellow, round sample. It includes, besides the ant, a dipteron and a collembolon; the ant is embedded in the stereotyped defence position with the gaster over the body; the tip of the gaster was removed probably by polishing, otherwise complete, but a crack, some bubbles and impurities prevent dorsal viewing of part of the head, of the propodeum and the pedicel.

Do-3826. A dark yellow 1.8x1.3 cm sample including only one ant. The specimen is complete and well visible but the head and the gaster have been strongly compressed dorsoventrally.

Do-3862. Dark yellow 2.0x1.1 cm sample containing only one ant. The specimen, separated and re-polished for the present study lacks only the left funiculus; the body alternates between completely transparent and very dark parts, probably as a result of heating. External morphology well visible.

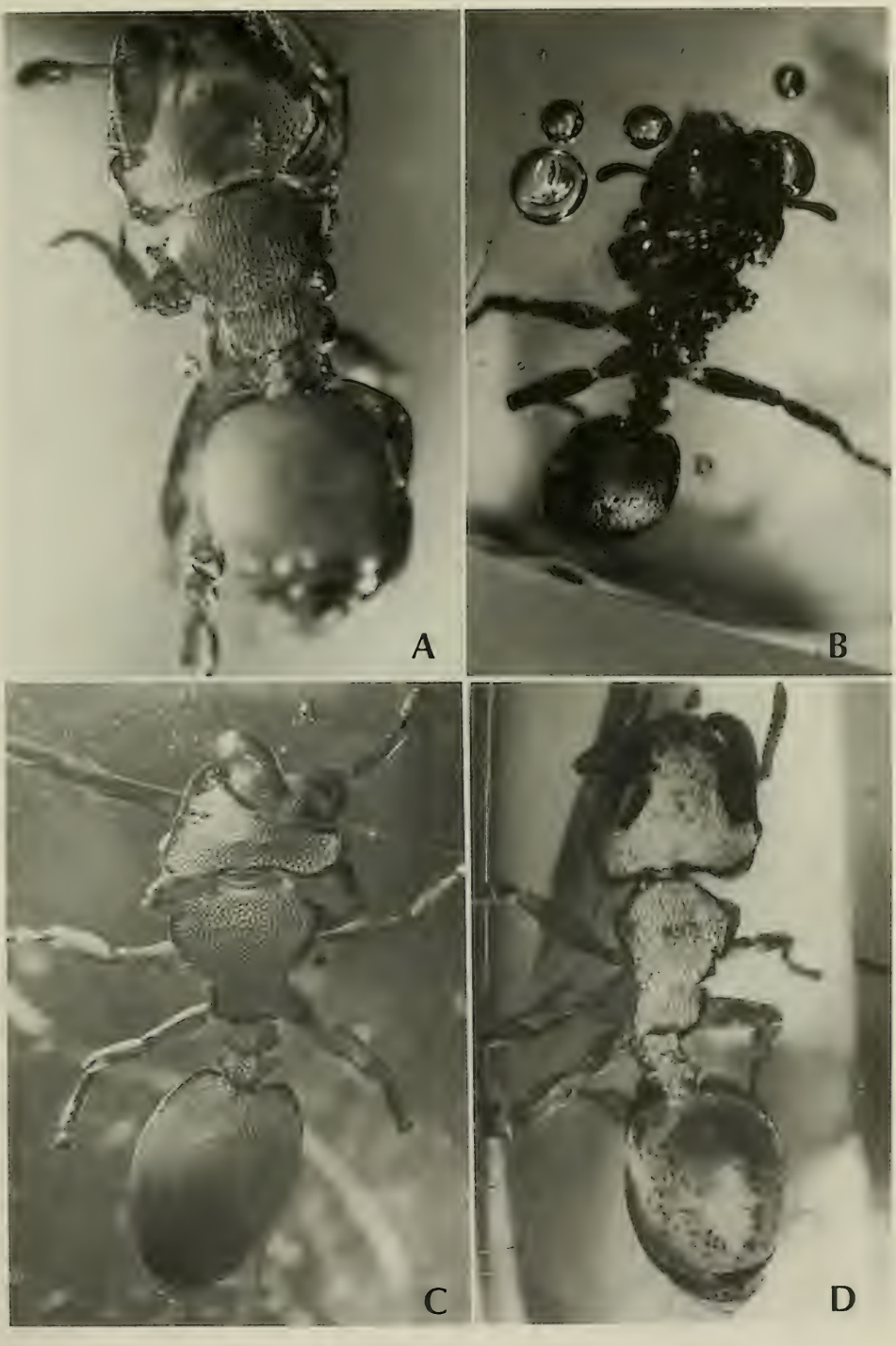


Fig. 7. Dominican amber. – A: Specimen Do-1980, dorsal view. – B: *Zacryptocerus alveolatus* VIERBERGEN & SCHEVEN, holotype, dorsal view. – C: Specimen Do-506, dorsal view. – D: Specimen Do-5317, dorsal view.

Do- 3936. 2.1x1.3 cm dark yellow sample containing the ant which has been separate and re-polished for study. The specimen lacks the tip of the abdomen, otherwise it is complete and well visible.

Do-3978. Dark, elongate (3.5x1.5 cm) specimen in which many soil particles, fragments of plant tissues, insect excrements, 1 *Azteca* worker and one cephalotine worker are included. The cephalotine has the left side close to the amber surface and is intact and well visible.

Do-3980. A 2.5x2.0 cm dark yellow sample embedding several soil particles, insect excrement, two collembola, a beetle prothorax with the legs and a single ant. The ant has been separate and re-polished for the present study; it appears intact and examination is practically not affected by the presence of a few minor air bubbles.

Do-4162. Fragment of a larger light yellow amber sample, cut and re-embedded in polyester (Vosschemie Gießharz GTS ®). The ant included in it is in the stereotyped defence posture with the gaster raised over the main body axis. The specimen is intersected by one longitudinal amber fissure but is intact and well visible from all sides (Fig. 16 B).

Do-4163. Obviously part of a larger amber sample, cut and re-embedded in polyester (Vosschemie Gießharz GTS ®). The single ant included is well visible in frontal, dorsal and lateral view (Fig. 13 D). The head bears a pair of symmetric round incisions over the vertexal angles which we interpret as artificial. The mesosoma is intersected by three transverse, slightly different amber layers which might have produced some deformation in the reconstruction of Fig. 127.

Do-4164. Fragment of a larger light yellow amber sample with dark layers, cut and re-embedded in polyester (Vosschemie Gießharz GTS ®). Several longitudinal and lateral fissures around the ant body allow optimal vision only of the head in dorsal view.

Do-4165. Small, light yellow sample, probably a fragment of a larger amber sample, cut and re-embedded in polyester (Vosschemie Gießharz GTS ®). The single ant included lacks the left pro- and meso- tarsi and bears some soil particles close to the abdominal tip; otherwise complete and well visible (Fig. 10 C).

Do-4210. Yellowish 1.6x1.0 cm sample containing a spider exuvia and 4 cephalotine workers (Fig. 5 A) as follows: 4210-1 touching the amber surface with the left side; left antenna partly missing. 4210-2 with a transverse fissure over the head, legs folded under the body, gaster bent ventrally towards the head, mesosoma covered by fungal hyphae. 4210-3 gaster between the mouthparts and the gaster of specimen 4210-2, head practically covered by fungal hyphae. 4210-4 body partly covered by fungal hyphae and (?) fragments of spider net, head in dorsal view well visible.

Do-4214. A 0.8x0.8 cm yellow amber sample with darker layers and containing only one ant worker. Left foretarsus missing, otherwise complete. Dorsal vision rendered difficult by the dark layers and a few longitudinal fissures.

Do-4230. Yellow sample 1.7x1.5 cm cut and re-polished to better observe the ant. The ant specimen bears some minor damage to the left antenna and cheek; a few minor fissures in the amber around the ant body and an irregular distribution of the gaseous film around the body render viewing difficult, though all relevant structures have been observed.

Do-4479. Oval, 1.7x1.1 cm dark yellow sample containing the ant with an insect leg between its legs and a few impurities. The ant specimen is surrounded by some air bubbles enabling proper vision only from the dorsum (Fig. 12 D).

Do-4480. 1.3x1.0 cm dark yellow sample embedding soil particles, vegetable fragments, an *Azteca* and a cephalotine worker. The cephalotine worker has been separate and re-polished for the present study and results well visible from all sides (Fig. 5 B).

Do-4637. Yellow, 1.9x1.2 cm sample containing two collembola and the ant. The latter has been separated and re-polished for the present study and it is included in the stereotyped defence position with the gaster over the major body axis. Good viewing from all sides (Fig. 11 D).

Do-4640. 2.5x2.6 cm, yellow sample containing several soil particles, a dipteron, insect fragments, a head capsule (probably *Azteca*) and a cephalotine worker. The latter is complete and well visible in spite of a few soil particles over the cephalic disc.

Do-4711. 6.5x2.5 cm, orange, not very transparent sample embedding three diptera, insect legs, and several cracks and air bubbles. The only ant in it has been separated and re-polished

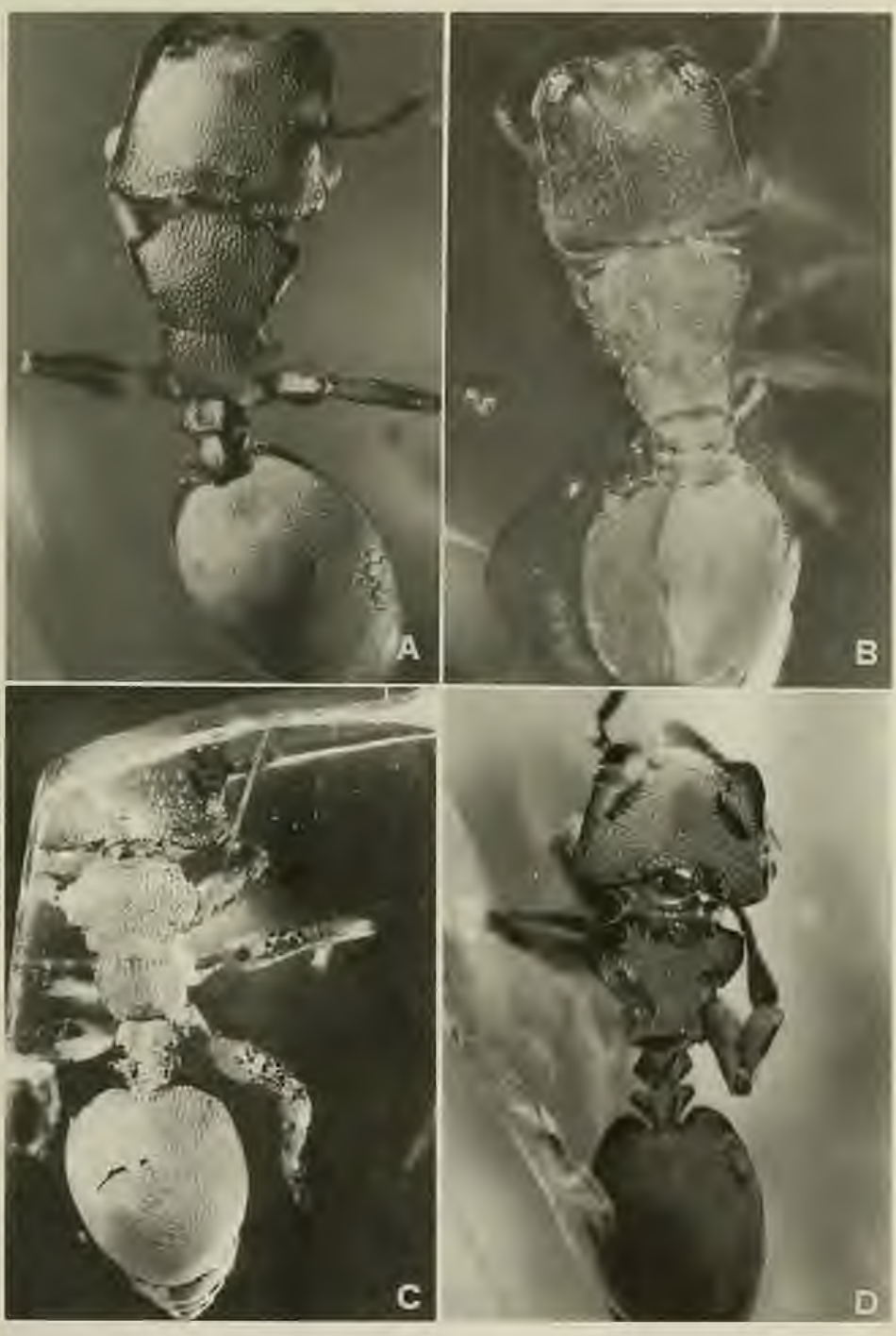


Fig. 8 Dominican amber. – A: Specimen Do-5544, dorsal view. – B: Specimen Do-2455, dorsal view. – C: Specimen H 10-116 J, dorsal view. – D: Specimen Do-5075, dorsal view.

for the present study: it appears intact though visibility is less good than in other specimens due to the presence of small air bubbles and impurities.

Do-4935. Fragment of a larger amber sample re-enclosed between two microscope cover slides. The ant specimen lacks the right fore- femur and tarsus and appears very darkened and internally destroyed, probably by heat.

Do-4962. 4.0x3.3 cm reddish sample including a cephalotine worker, 2 soldiers and 2 workers of *Pheidole*, an *Oxyidris* worker, a small *Azteca*, a cricket, a moth, 2 small flies, a spider and other insect remainings. The cephalotine, separated and re-polished for the present study, is affected by the presence of some air bubbles on its ventral side but allows very good dorsal examination.

Do-5075. Dark yellow, slightly opaque 2.1x2.1 cm sample. Lateral and ventral vision of the ant, which has been separated and re-polished for the present study, is rendered difficult by amber fissures and air bubbles. Good dorsal visibility, except the mouthparts which are entirely enclosed in an air bubble (Fig. 8 D).

Do-5163. 1.7x1.1 cm yellow sample including an ant, a small roach and fragments of insect integument. After cutting and re-polishing of the amber sample the ant appears well visible in dorsal view; lateral view slightly reduced by the presence of a small air bubble on both sides of the pedicel (Fig. 5 D).

Do-5226. 1.0x0.8 cm oval, dark yellow sample containing only the ant. Several fissures in amber render observation less than optimal, though all important details can be examined.

Do-5317. 2.2x1.6 cm yellow sample including the abdomen with part of the legs of an insect (fly?), and the ant. The latter is close to the surface with its left side, and part of the foretibia and the foretarsus, a longitudinal portion of the middle tibia, and the hind tibia and tarsus are missing. The specimen has been cut and re-polished for the present study rendering observation of all the remaining parts good (Fig. 7 D).

Do-5383. 3.3x2.2 cm yellow sample embedding insect excrement and fragments and the ant. The ant, separately cut and polished for the present study, appears in the "turtle" stereotyped defence position, intact and well visible in spite of being positioned across two different amber layers (Fig. 15 C).

Do-5487. 1.8x1.3 cm yellow sample embedding a small beetle and an ant. The ant has been separated and re-polished for the present study and appears intact and well visible from all sides (Fig. 16 D).

Do-5492. 1.7x1.0 cm yellowish sample containing only one cephalotine worker and an *Azteca* cephalic capsule. The cephalotine body is surrounded laterally by a short, flat fringe of "dendritic" air inclusions which do not prevent optimal observation (Fig. 6 A).

Do-5544. 2.1x1.6 cm yellow sample containing only an ant excellently preserved conditions and allowing good observation dorsally and from both sides (Fig. 8 A).

Dominican copal

Do-3014. Very light 3.0x1.6 cm piece containing 6 diptera, a roach and one cephalotine ant. The latter is intact but has the gaster and the legs bent ventrally. Few darker veins of the copal close to the ant body may render examination of some details slightly difficult.

DoC-3566. Light 1.5x0.9 cm sample containing, in addition to the ant, a dipteron. The copal fragment is affected by several air bubbles and minor cracks but dorsal and lateral vision of the ant are very good (Fig. 12 B).

Mexican amber

Mx-391. 1.8x2.0 cm, pointed, irregular, yellow sample containing a cephalotine worker, 10 *Crematogaster* workers, partly in very bad shape, and soil particles. The cephalotine, separate and re-polished for the present study, appears only slightly deformed and substantially intact. Both dorsal and lateral views are satisfactory (Fig. 14 B).

Fig. 9. Dominican amber. – A: Specimen H 10-117, dorsal view. – B: Specimen H 10-117, lateral view. – C: Specimen Do-3581, dorsal view. – D: Specimen Do-3581, lateral view.

From the GOPC

Dominican amber

H 10-105. 3.4x4.0 cm, light yellow sample containing five Diptera, a mite, different insect fragments, a badly preserved dolichoderine worker, a headless worker of (?) *Wasmannia*, and a cephalotine worker. The latter is complete, dorsoventrally compressed, but only slightly deformed in dorsal view (Fig. 14 A).

H 10-116. Yellow, slightly opaque, 3.5x7.0 cm sample containing several plant and insect fragments, a springtail, a *Brachymyrmex* worker, and three cephalotine workers separate and re-polished for the present study. One specimen (H 10-116-1) lacks the femoro-tibial articulation of the third right pair of legs, is rolled around a large piece of insect excrement but allows very good dorsal vision. The second specimen (H 10-116-2) has the gaster bent ventrally towards the head and the left side of the gaster has been partially removed by polishing; it is suitable, however, for dorsal vision. The third specimen (H 10-116-3) is represented only by a nearly complete mesosoma with the right posterior leg.

H 10-116 A. 2.0x1.4 cm yellowish specimen containing a beetle, a hair, a mite and the ant. The latter appears slightly compressed dorsoventrally but very suitable for dorsal, lateral and ventral observation (Fig. 10 B).

H 10-116 B. 1.9x1.3 cm yellowish specimen containing a microhymenopteron, a dipteron, insect excrement, a few soil particles and an ant. This is affected by three transverse fissures in amber respectively over the head, the pronotum and the gaster. The fissures do not prevent examination of the specimen which is intact and in good shape (Fig. 6 C).

H 10-116 C. Yellowish-brown, 2.5x1.1 cm sample embedding a piece of leaf, a large excrement, different insect excrement, a small fly, different insect fragments, a mite, two beetles, an ant gaster, two *Diplorhoptrum* workers, a worker of *Technomyrmex caritatis* BRANDÃO et al., a cephalotine worker. This is partly covered by the large excrement but is in excellent shape and dorsal and frontal views are very good.

H 10-116 D. 2.2x1.9 cm brown sample containing different insect fragments, a mite, a staphylinid beetle an *Azteca* cephalic capsule, and a cephalotine worker which has been cut and re-polished for the present study. This appears in excellent shape and very suitable for observation from every side (Fig. 6 B).

H 10-116 E. A 1.8x1.1 cm yellow sample containing only the ant. It has been reduced in size and re-polished for the present study allowing very good observation of the ant specimen in spite of some minor fissures in amber (Fig. 6 D).

H 10-116 F. 1.3x1.2 cm brown sample containing many soil particles, plant tissue, two coleoptera, a microhymenopteron, different insect fragments and an ant which has been separated and re-polished for the present study. Good dorsal view in spite of the proximity of some soil particles.

H 10-116 G. Yellow, 0.5x0.8 cm sample re-polished for the present study. It contains only the ant, intact and well visible from all sides.

H 10-116 H. Yellow, 1.5x1.5 cm sample containing only a small fragment of plant tissue and the ant lacking a small portion of the abdominal tip. The specimen appears dark and deformed; the head partly covered by an air bubble and the gaster covered by spider silk(?).

H 10-116 I. Yellow, 2.6x1.6 cm sample embedding several soil particles, insect excrement, a piece of hair, parts of plant tissue, several insect fragments including a large (?ponerine) ant mandible, a cephalic capsule of *Pseudomyrmex*, a mesosoma with legs of *Odontomachus spinifer*, three Diptera, a worker of *Azteca*, a worker of *Technomyrmex caritatis* BRANDÃO et al., and a cephalotine worker missing part of the right fore tibia and tarsus, compressed dorsoventrally but suitable for study.

H 10-116 J. A 6x1.3 cm, yellow sample containing a fly, a bug and a cephalotine worker. The latter, missing the left funiculus and mid tibia, has been separated and re-polished for the present study allowing very good vision from all sides (Fig. 8 C).

H 10-117. 3.0x2.0 cm yellow sample embedding soil particles, insect excrement, a plant fragment, a dipteron and a single worker ant lacking the tip of the abdomen, otherwise very well preserved and perfectly visible (Fig. 9 A & B).

H 10-118. Light yellow 3.5x2.0 cm sample containing a single worker ant with the body entirely free from the tiny gaseous film to be found around most amber cephalotine speci-

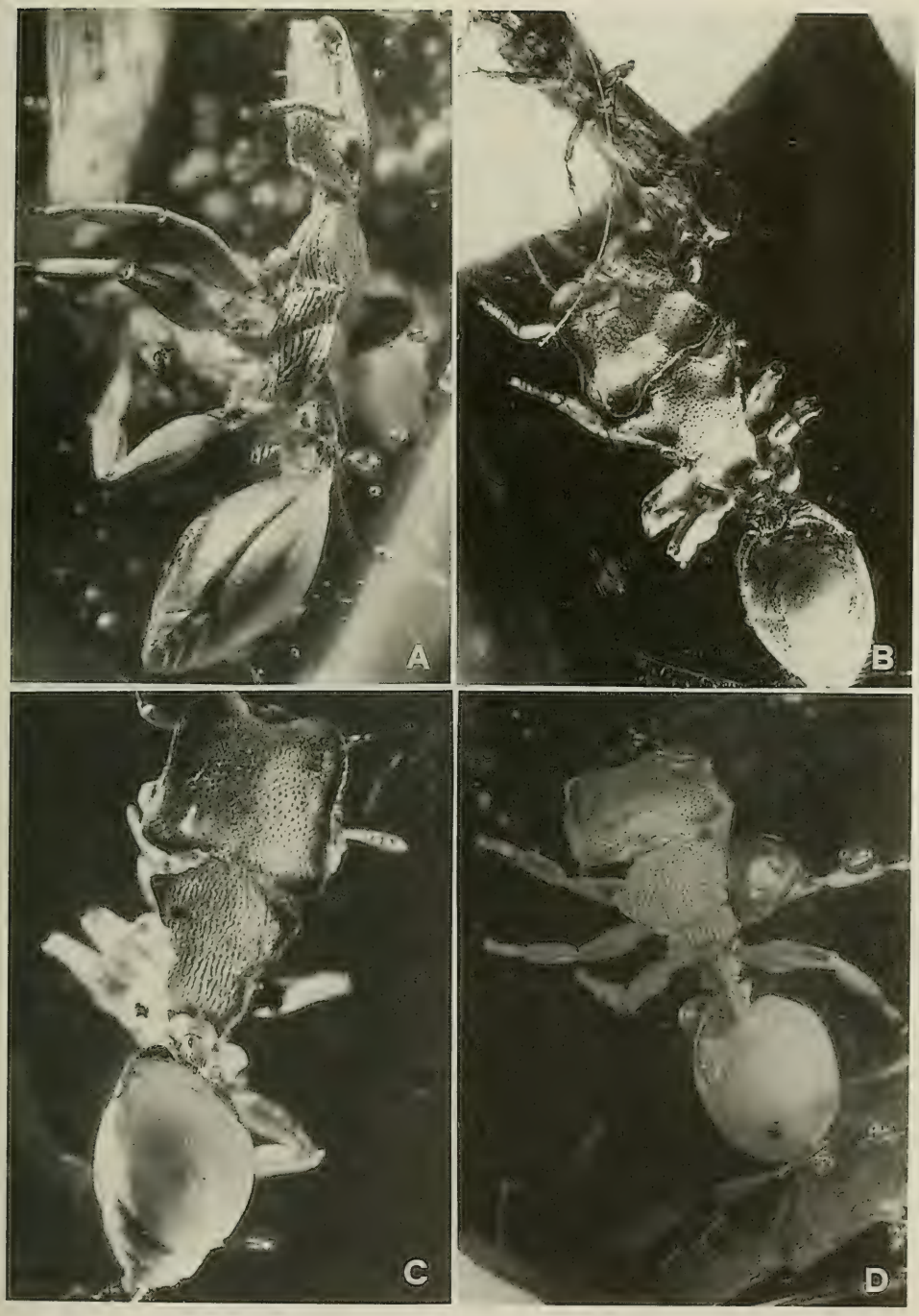


Fig. 10. Dominican amber. – A: Specimen Do-3316, lateral view. – B: Specimen H 10-116 A, dorsal view. – C: Specimen Do-4165, dorsal view. – D: Specimen PE 110, dorsal view.

mens; the gaster is bent ventrally towards the head; preservation conditions and visibility excellent (Fig. 13 A – C).

H 10-119. Light yellow 3.5x2.2 cm sample including two diptera, three microhymenoptera, a male of *Proceratium*, a male of Ponerinae and a well visible, intact cephalotine worker separated and re-polished for the present study (Fig. 14 C).

H 10-120. Yellow 2.0x1.2 cm sample containing only an intact ant worker; some transversal fissures in amber around the ant body make observation of details difficult.

H 10-121. 3.0x1.5 cm light yellow sample embedding soil particles, insect excrement, fragments of plant tissue and a single incomplete soldier of cephalotine. The latter, separate and re-polished for the present study, is embedded in the stereotypic defence posture with the gaster over the body axis. Part of the left foretibia and left mesotarsus missing, otherwise complete and well visible (Fig. 11 A & C).

Mexican amber

Mex. 1. 2.0x1.5 cm yellow sample containing a micro-hymenopteron, vegetable tissue, caterpillar excrement and a worker ant. The piece has been cut into three parts to improve vision of the ant specimen. Some body parts, like the tip of the left last antennal joint, most of the left fore leg, both mid coxae and trochanters, hind coxae and trochanters, left hind tibia, and right hind femur and tibia are compressed or damaged to an extent rendering exact observation difficult. Fore and mid femora only slightly damaged. Other body parts well preserved and visible (Fig. 15 A & B).

Mex. 2. 4.2x2.7 cm brown sample containing numerous soil particles, fragments of leaves and plant tissue, different insect fragments, three diptera, and three cephalotine workers separated and re-polished for the present study as follows: Mex. 2-1 surrounded by several soil particles so as to be suitable only for observation in dorsal view; right border of the gaster missing; Mex. 2-2 nearly intact specimen (missing most of the mid left leg, tarsus of hind left leg , tibia and tarsus of the right hind leg) ventrally close to an amber fissure, very suitable for right lateral and dorsal observation (Fig. 14 D); Mex. 2-3 surrounded by several soil particles, without head, legs, and part of the left gastral lamella; structure of the mesosoma, petiole and gaster well visible.

H 10-201. Small sample of yellowish amber containing only a cephalotine ant. The ant is nearly complete except for the last right antennomere and the right metatarsus. Observation and description of the specimen are nonetheless rendered difficult by a set of fissures covering in part the ant body and by deformations of the latter. Some fissures cover great parts of the gaster which can be observed properly only from the ventral side. The following, detailed, description of the preservation conditions of the different parts should aid in understanding the reconstruction necessary to obtain the drawing of Fig. 195. We suggest comparing this description with the figure legend. Head slightly deformed and asymmetric; head margins slightly broken, particularly on the left side; sculpture in general well visible, particularly in the anterior and posterior parts, but sometimes apparently deformed; left funiculus strongly compressed. Mesosoma slightly deformed as is the head; sculpture well visible only on the anterior part of the pronotum and on the transparent lateral lamellae; remaining parts dark with the microsculpture barely visible; vision of the petiole rendered difficult by an amber fissure, its sculpture visible on the lateral expansions but just perceivable on the rest; postpetiole difficult to observe in dorsal view but its contour is well visible in ventral view, its dorsal microsculpture visible only in a small part of the base. Forelegs; the right leg better preserved than the left one but the femur and tibia are respectively strongly and lightly depressed; tarsomeres 2-5 better visible in the left leg. Midlegs; both femora and other parts strongly deformed, the contour of the right tibia and tarsus is probably unaltered. Hindlegs; right femur strongly deformed, the right one well preserved but visible only in side view; both tibiae well visible but the left one is compressed; left tarsus well visible. Gaster compressed on the right side in a way probably affecting the contour; microsculpture generally well visible.

From the JSHC

Dominican amber

Exocryptocerus serratus VIERBERGEN & SCHEVEN, holotype. Yellow sample (0.9x1.6 cm) with only the ant included. Specimen in good shape missing only the last three funicular joints of the left antenna.

Exocryptocerus elevatus VIERBERGEN & SCHEVEN, holotype. Yellow sample (1.6x2.7 cm). I In addition to the ant, a microhymenopteron and three minute mites are also included. The ant is in excellent shape (Fig. 17 A).

Exocryptocerus truncatus VIERBERGEN & SCHEVEN, holotype. Yellow sample (1.7x1.8 cm). Besides the ant, in excellent shape, only a few air bubbles are visible in the amber (Fig. 17 B).

Exocryptocerus jansei VIERBERGEN & SCHEVEN, holotype. Yellow sample (1.5x2.0 cm) with only few impurities. The specimen is in good shape (Fig. 11 B).

Zacryptocerus integerrimus VIERBERGEN & SCHEVEN, holotype. Light yellow sample (1.7x3.0 cm) containing, in addition to the ant, several minute impurities. The ant misses only part of the first left funicular joint; otherwise in excellent shape, though it is surrounded by a layer of amber with different diffraction index rendering difficult observation from all sides (Fig. 18 A).

Zacryptocerus squamosus VIERBERGEN & SCHEVEN, holotype. Yellow sample (1.0x1.5 cm) containing only a few air bubbles and the ant in good shape, except for part of the right frontal carina, missing. The specimen is clearly visible in dorsal view. A major fissure prevents observation of the left profile.

Zacryptocerus squamosus VIERBERGEN & SCHEVEN, paratype. Yellow sample (0.8x1.7 cm). Inclusions: a spider, 8 mites and a small insect (dipteron?) over the head of the ant. The ant (missing most of the left hind leg except the coxa and the tarsus of the right hind leg) is suitable for left side lateral examination and dorsal examination of the mesosoma (Fig. 17 C).

Zacryptocerus squamosus VIERBERGEN & SCHEVEN, paratype. Yellow sample (0.9x1.4 cm) with many fissures preventing part of the vision of the ant, otherwise in excellent shape.

Zacryptocerus pseudoaztecus VIERBERGEN & SCHEVEN, holotype. Yellow sample (0.6x1.7 cm). The ant is the sole inclusion and in good shape in spite of missing the mid and hind right legs (Fig. 17 D).

Zacryptocerus alveolatus VIERBERGEN & SCHEVEN, holotype. Light yellow (1.5 x2.0 cm) sample containing only the ant and air bubbles. The ant specimen is burned and with partly fragmented integument (Fig. 7 B).

From the MCCB

Dominican amber

0025. Large (8.5x5 cm) yellowish brown sample with several cracks and containing ca. 25 diptera, one orthopteron, 1 *Proceratium* winged gyne, a myrmicine male and a cephalotine worker. The latter is free from the gaseous film, close to the surface, very well preserved and visible in dorsal view without further cutting or polishing the amber sample (Fig. 18 B).

From the MCZC

Dominican amber

All the MCZC Cephalotini specimens have been arbitrarily numbered by us as MCZC-1, MCZC-2, etc. for the purpose of the present study. Some of these specimens are of particular value because they bear a precise locality label with the mine of provenance. The location of the amber mines mentioned here can be found in the maps published by BARONI URBANI & SAUNDERS (1982) and POINAR (1992).

MCZC-1. Dark yellow sample 3.5x3.0 cm in size containing a cephalotine worker, soil particles, insect excrement and air bubbles. The sole ant lacks the right part of the vertex and pronotum, and the dorsal part of the gaster.

MCZC-2. Small (0.8x1.1 cm) yellow, sample. The inclusions are a complete cephalotine worker and an unidentified ant gaster + hind legs. Labelled as *Exocryptocerus serratus* VIERBERGEN & SCHEVEN by G. Vierbergen and explicitly mentioned in VIERBERGEN & SCHEVEN (1995). Must be considered a paratype.

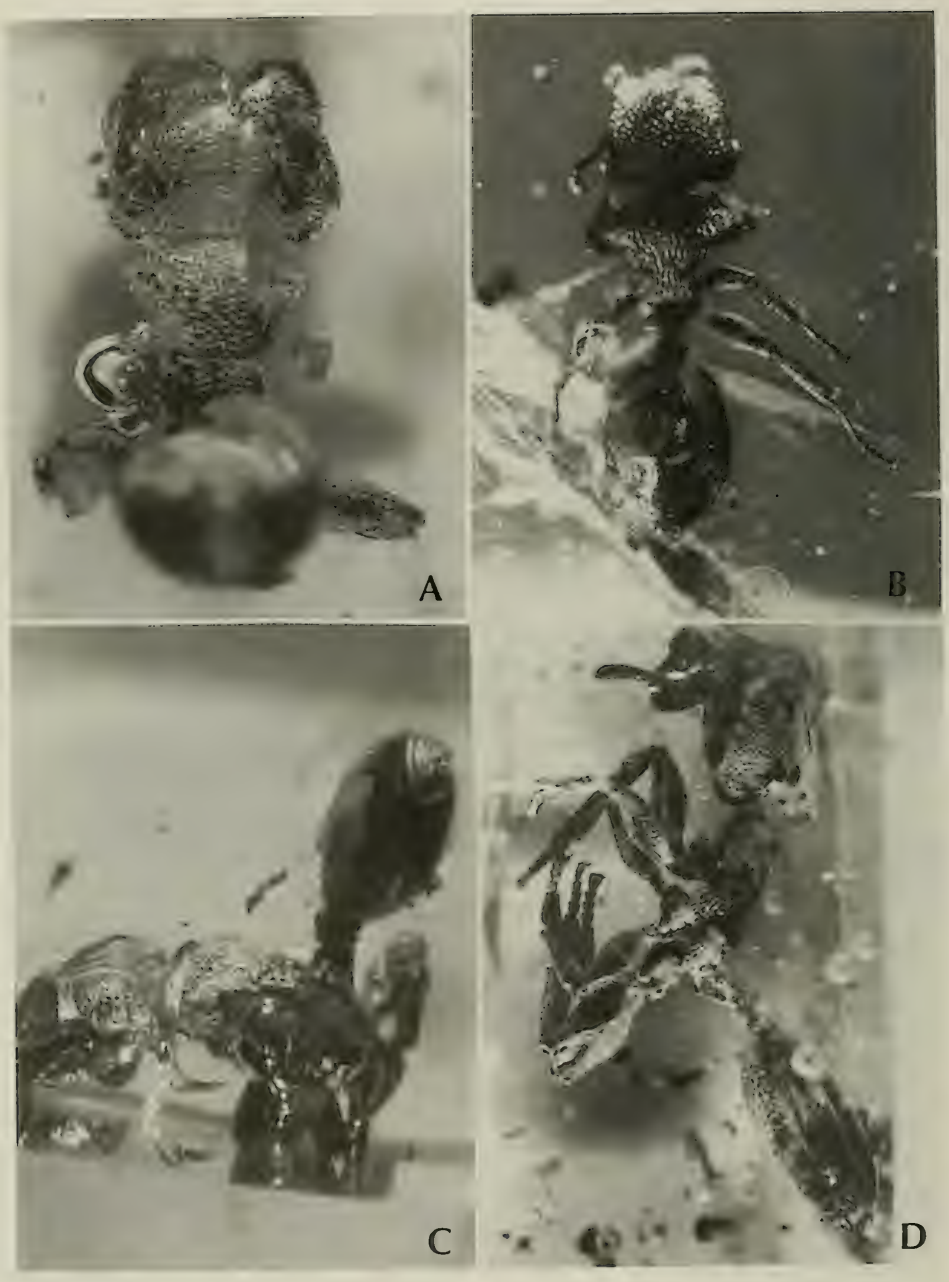


Fig. 11. Dominican amber. – A: Specimen H 10-121, dorsal view. – B: *Exocryptocerus jansei* VIERBERGEN & SCHEVEN, holotype, dorsal view. – C. Specimen H 10-121, lateral view; this ant has the gaster raised at 90° over the major body axis; this is likely to be a stereotype defence posture known only from a small number of Recent species which, when attacked or disturbed, assume the same posture to release in the air a repellent pheromone. – D: Specimen Do-4637, lateral view.

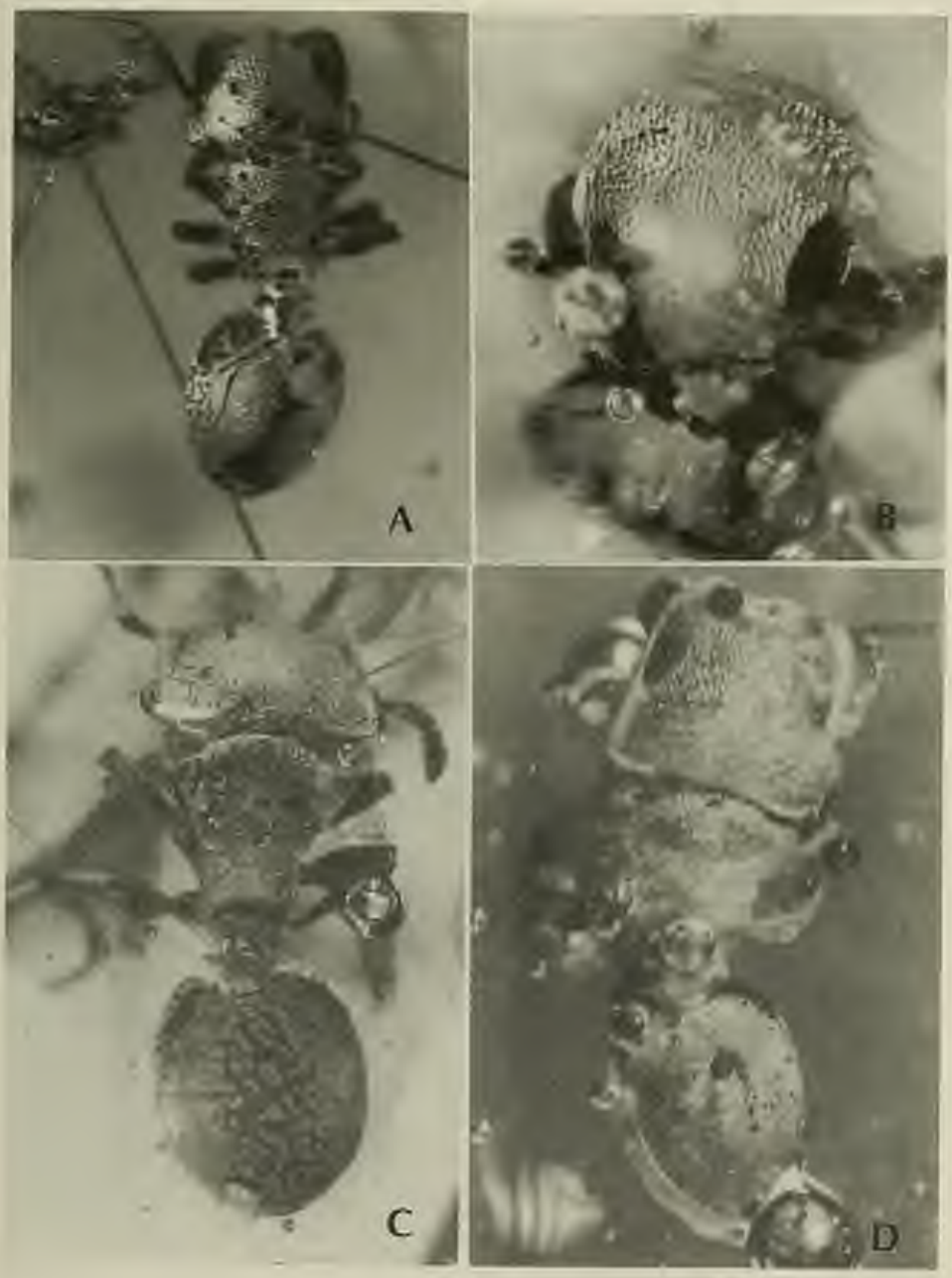


Fig. 12. Dominican amber and copal. – A: Specimen Do-3792 (amber), dorsal view. – B: Specimen DoC-3566 (copal), frontal view of the head. – C: Specimen Do-3326 (amber), dorsal view. – D: Specimen Do-4479 (amber), dorsal view.

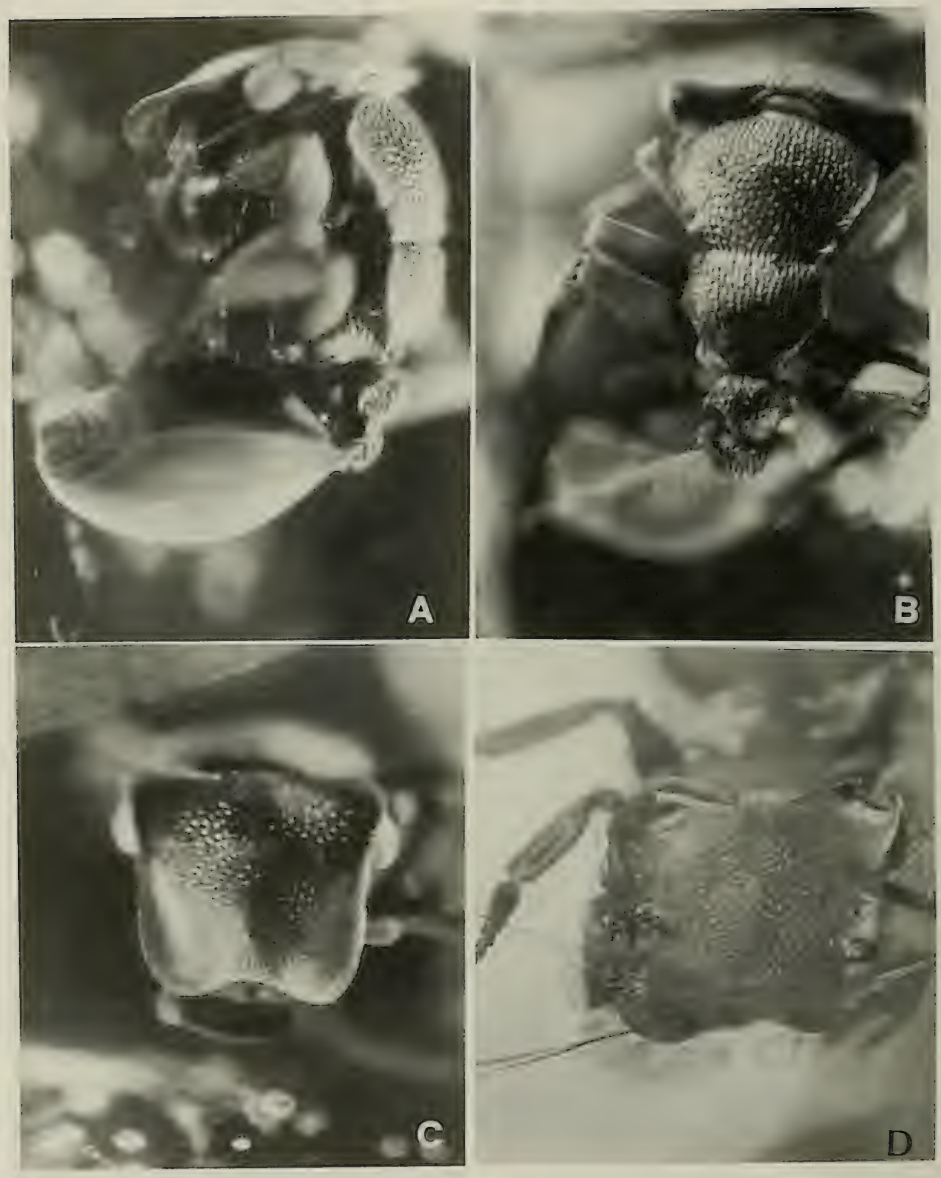


Fig. 13. Dominican amber. – A: Specimen H 10-118, lateral view. – B: Specimen H 10-118, dorsal view. – C: Specimen H 10-118, head in frontal view. – D: Specimen Do-4163, head in frontal view.

MCZC-3. Small, yellow sample (1.3x1.7 cm) affected by a major fissure and containing an intact ant worker and few impurities. Labelled as *Zacryptocerus pseudoaztecus* by G. Vierbergen and explicitly mentioned as paratype in VIERBERGEN & SCHEVEN (1995).

MCZC-4. Small, yellow sample (1.5x1.3 cm) with many fissures. The sole inclusion is a cephalotine worker. Labelled as *Exocryptocerus jansei* VIERBERGEN & SCHEVEN by G. Vierbergen and explicitly mentioned in VIERBERGEN & SCHEVEN (1995). Must be considered a paratype.

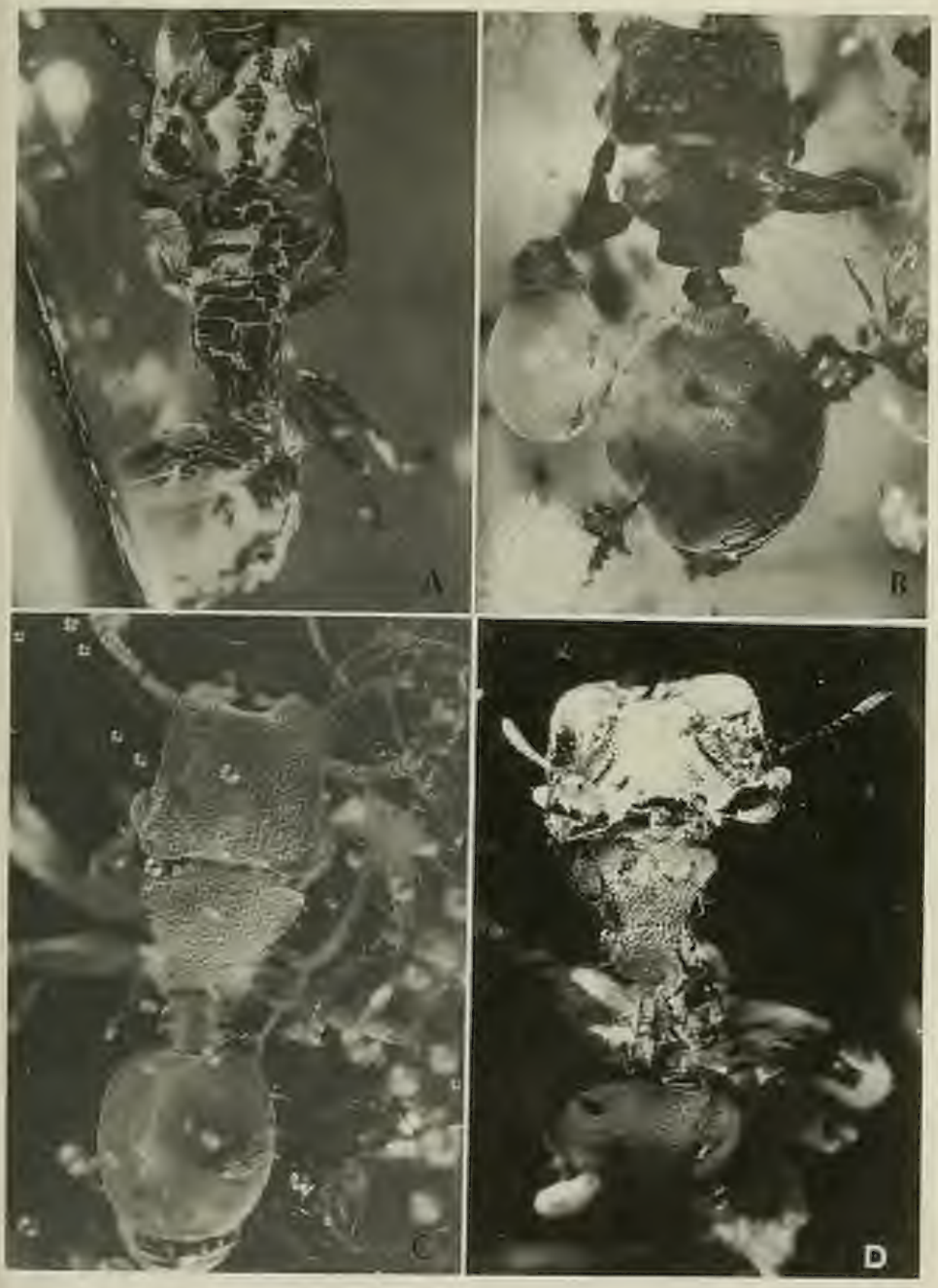


Fig. 14. Dominican and Mexican amber. – A: Specimen H 10-105 (Dominican), dorsal view. – B: Specimen Mx-391 (Mexican), dorsal view. – C: Specimen H 10-119 (Dominican), dorsal view. – D: Specimen Mex-2-2 (Mexican), dorsal view.

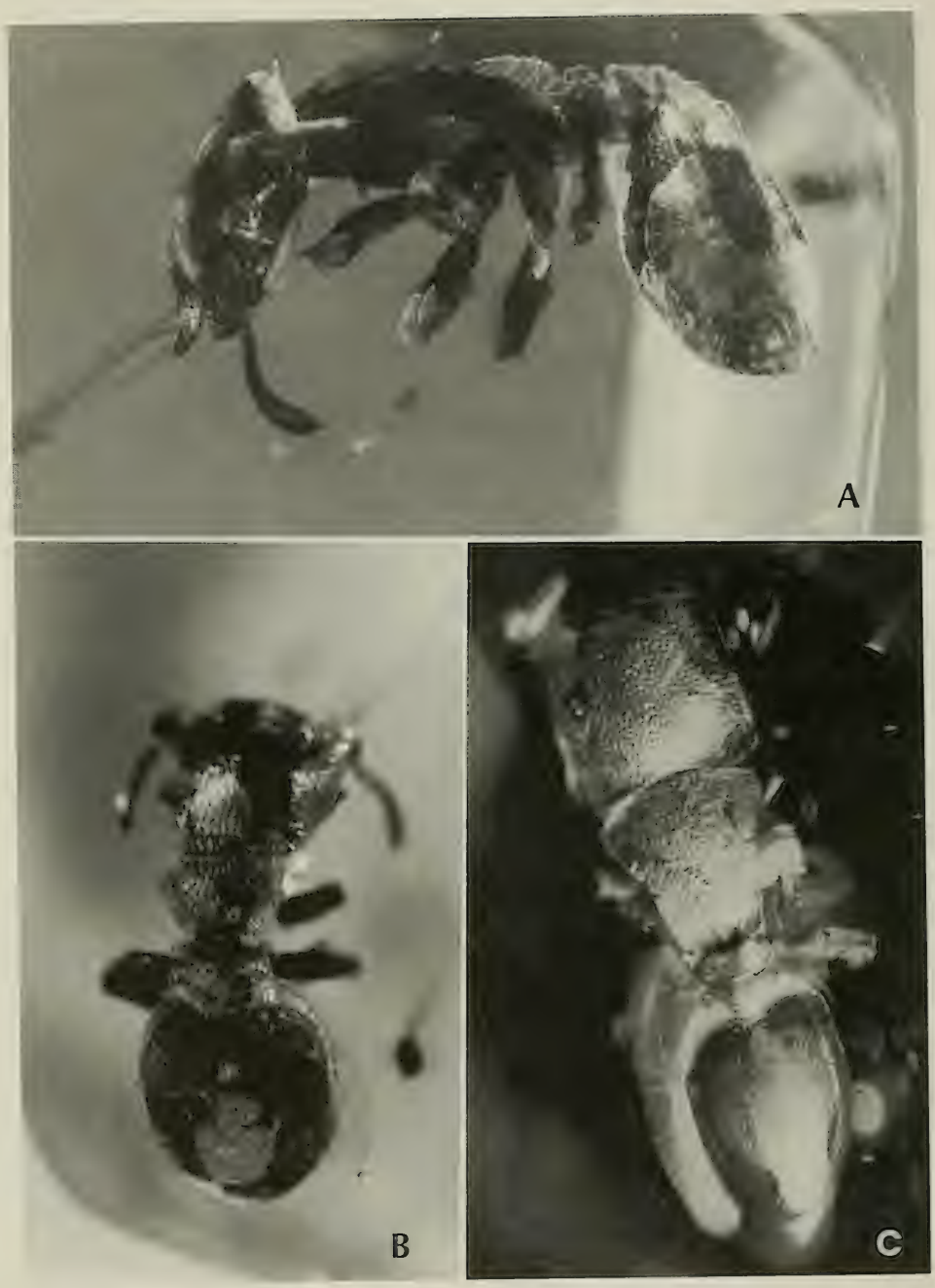


Fig. 15. Mexican and Dominican amber. – A: Specimen Mex-1 (Mexican), lateral view. – B: Specimen Mex-1 (Mexican), dorsal view. – C: Specimen Do-5383 (Dominican), dorsal view.

MCZC-5. Small, yellow sample (1.2x1.4 cm) with many fissures. It includes an intact cephalotine worker. Labelled as *Zacryptocerus squamosus* Vierbergen & Scheven . Should be considered as a paratype.

MCZC-6. Small, yellow sample (1.4x1.3 cm). The sole animal inclusion is cephalotine worker. Labelled as *Zacryptocerus* sp. by G. Vierbergen but not explicitly mentioned in VIERBERGEN & SCHEVEN (1995).

MCZC-7. Dark yellow 2.3x1.8 cm sample. It includes several air bubbles and a cephalotine worker, another poorly visible myrmicine worker (probably *Wasmannia*), three mites, an unidentified insect and excrements. Labelled as *Zacryptocerus* sp. by G. Vierbergen but not explicitly mentioned in VIERBERGEN & SCHEVEN (1995).

MCZC-8. 1.2x0.8 cm yellow sample containing only a cephalotine ant missing the right antenna. The ant, particularly the appendages, appears to be either covered by a thick gaseous film or to be inflated (a pupa?). Labelled as *Zacryptocerus* sp. by G. Vierbergen but not explicitly mentioned in VIERBERGEN & SCHEVEN (1995).

MCZC-9. *Zacryptocerus obscurus* VIERBERGEN & SCHEVEN, holotype. Yellow, oval (2x1.3 cm) very clear sample crossed by a plane of dark (pyrite?) dendritic formations. It contains only a cephalotine worker in excellent shape (Fig. 16 C).

MCZC-10. Yellow 2.2x1.3 cm sample affected by several fissures. It contains only an intact cephalotine worker. Labelled as *Zacryptocerus* sp. by G. Vierbergen but not explicitly mentioned in VIERBERGEN & SCHEVEN (1995).

MCZC-11. From the amber mine La Toca (R. Harrison). Dark yellow, small (1.6x0.9 cm) sample affected by longitudinal layers of bubbles and detritus. The sole insect included is a cephalotine worker. Labelled as *Exocryptocerus serratus* VIERBERGEN & SCHEVEN by G. Vierbergen . Must be considered a paratype.

MCZC-12. Yellow sample of 1.5 x1.0 cm from the Santiago province. It contains a cephalotine worker in good shape (left part of the gaster missing) and two unidentified insects. Labelled *Zacryptocerus* sp. det G. Vierbergen.

MCZC-13. Yellow sample 1.3x0.8 cm from the amber mine La Toca containing only a cephalotine worker in good shape and missing only the last three right tarsomeres of the hind leg.

MCZC-14. A light yellow sample 1.5x1.0 cm containing only an intact cephalotine worker.

MCZC-15. A light yellow sample 1.1x1.0 cm from the amber mine El Valle containing an intact cephalotine worker. The specimen is surrounded by a brown layer and some air bubbles rendering examination difficult.

MCZC-16. A light yellow sample 1.7x1.2 cm from the amber mine La Toca. It contains a cephalotine worker intact but difficult to observe because of a surrounding brown layer and fissures in amber.

MCZC-17. Yellow 1.2x0.7 cm sample with several air bubbles and containing a cephalotine worker in good shape.

MCZC-18. Yellow 2.0x1.4 cm sample from La Toca including an intact cephalotine and few soil particles.

MCZC-19. A yellow 1.2x0.9 cm sample from the amber mine La Toca containing a cephalotine worker in good shape and an unidentified insect. The vision is partly difficult for the presence of a transversal fissure.

MCZC-20. Yellow 1.2x1.0 cm sample from the Santiago province. It contains only few impurities and a cephalotine worker missing both hind femora, tibiae and tarsi, petiole, postpetiole and gaster.

MCZC-21. Yellow 2.6x2.4 cm sample containing a cephalotine worker, three Diptera, a small spider, an insect wing and air bubbles. The ant lacks three tarsomeres of the mid right leg and five tarsomeres of the right hind leg.

MCZC-22. Dark yellow sample 0.7x1.0 cm from the province of Santiago. It contains only one ant without femur, tibia and tarsus of the mid right leg. Vision of the specimen is rendered difficult by two fissures in amber.

MCZC-23. Dark yellow 2.6x1.7 m sample. It contains a cephalotine worker, several air bubbles and impurities.

MCZC-24. Yellow, transparent 2.3x1.5 cm sample from Yanigua, a small agglomeration 3

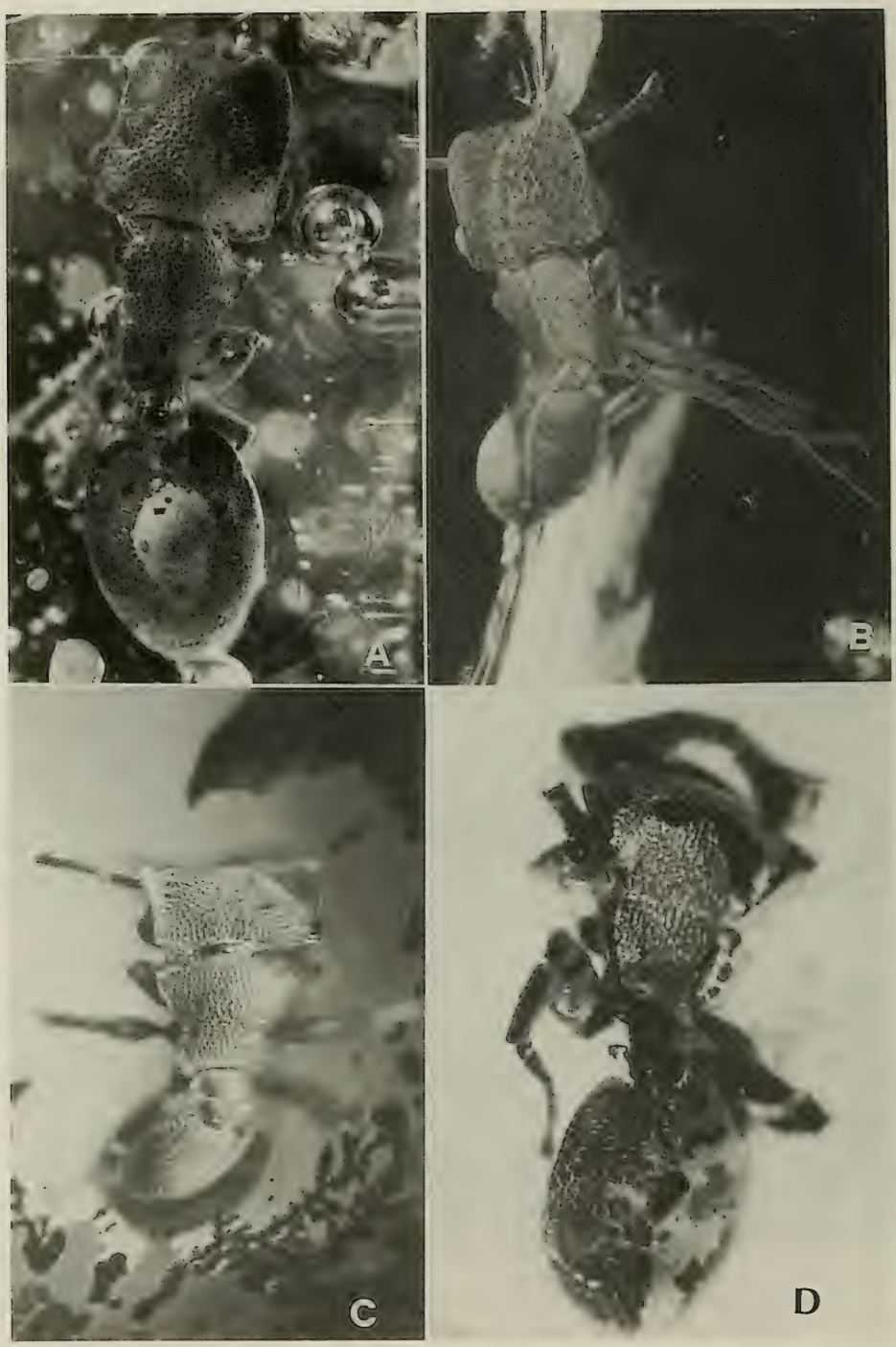


Fig. 16. Dominican amber. – A: Specimen Do-618-K, dorsal view. – B: Specimen Do-4162, dorsal view. – C: *Zacryptocerus obscurus* VIERBERGEN & SCHEVEN, holotype, MCZC-9, dorsal view. – D: Specimen Do-5487, dorsal view.

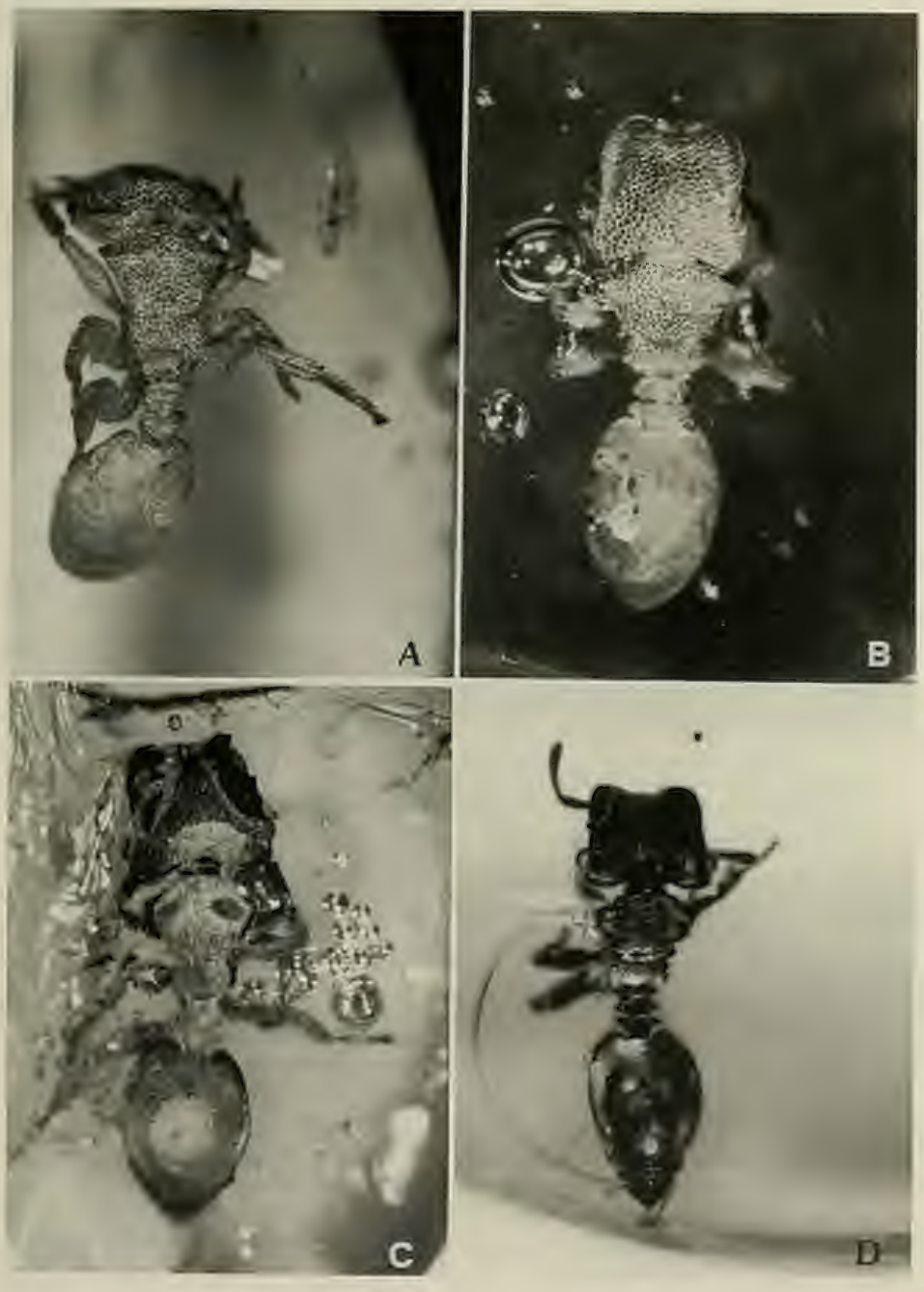


Fig. 17. Dominican amber. – A: *Exocryptocerus elevatus* VIERBERGEN & SCHEVEN, holotype, dorsal view. – B: *Exocryptocerus truncatus* VIERBERGEN & SCHEVEN, holotype, dorsal view. – C: *Zacryptocerus squamosus* VIERBERGEN & SCHEVEN, holotype, dorsal view. – D: *Zacryptocerus pseudoaztecus* VIERBERGEN & SCHEVEN, holotype, dorsal view.

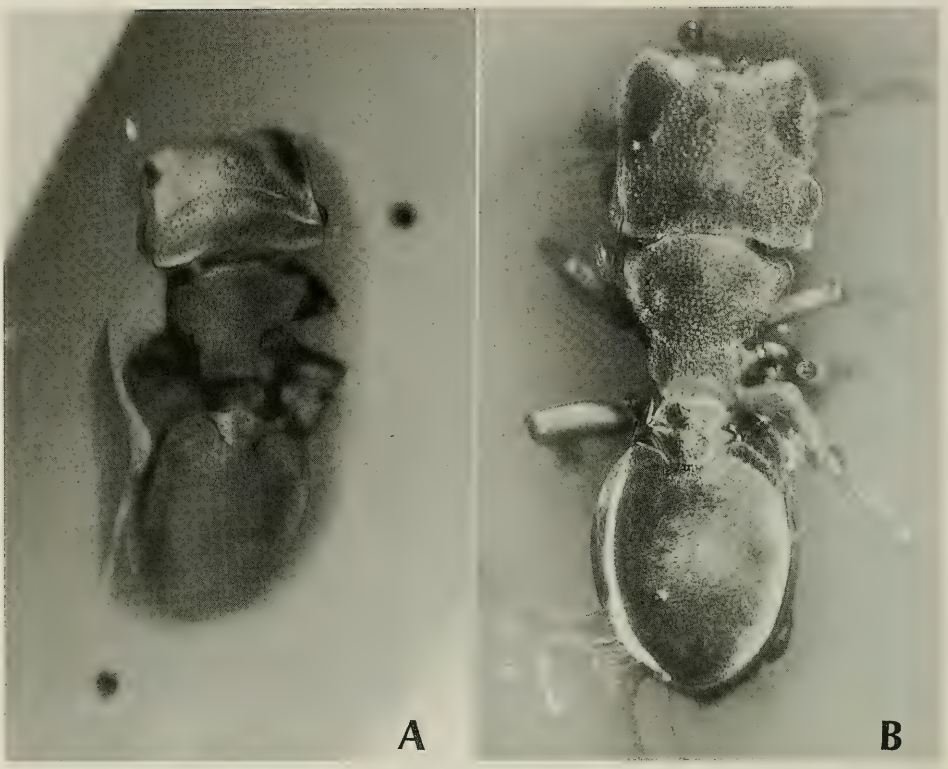


Fig. 18. Dominican amber. – A: *Zacryptocerus integerrimus* VIERBERGEN & SCHEVEN, holotype, dorsal view. – B: Specimen MCCB 0025, dorsal view.

km W of the mine El Valle. It contains nine Diptera, a *Technomyrmex* worker and an intact cephalotine worker.

From the NHMB

Dominican amber

All specimens originate from Dominican gift shops and were already cut and polished to enable good vision of the single ant specimen and excluding most of other inclusions. They are the following:

PE 110. Dark yellow amber. An air bubble on the right side of the mesosoma reduces lateral view, otherwise intact and very well visible specimen (Fig. 10 D).

PE 111. Yellowish amber. Very damaged specimen missing both terminal antennal joints, the left fore tarsus, the whole right fore leg, the left mid and hind legs, the hind right tarsomeres, and the tip of the gaster. Postpetiole detached from petiole, the latter fissured longitudinally. Some insect fragments.

PE 112. Dark yellow amber. Very well preserved and visible specimen except a transversal crack between petiole and postpetiole. Some soil particles and a fragment of an insect leg.

PE 114. Oval yellowish sample, 1.1x0.7 mm. The ant has been partly destroyed by polishing so that only hollow parts of the integument remain. Missing are the anterior part and the right side of the head, part of the right side of the mesosoma and the right legs, the right border of the gaster.

Most amber specimens have been cut and polished or re-polished by us to improve observation of the Cephalotini specimen(s) for the present study. Drawings and measurements have been made always after immersion in 66% sucrose solution. All the drawings are due to the talent and to the patience of Armin Coray.

The Recent material we used for comparison with the fossils is deposited in the following collections, given here with the relative coden as it will be used in the following text:

BMNH. The Natural History Museum, London. Courtesy of Mr. Barry Bolton.
CPCC. Centro de Pesquisa do Cacao, CEPLAC, Itabuna, Bahia. Courtesy of Dr. Jacques H. C. Delabie.
INPA. Instituto Nacional de Pesquisas da Amazônia. Courtesy of Dr. José Albertino Rafael and Dr. Ana Y. Harada.
JSHC. Collection Joachim Scheven, Hagen, Germany. Courtesy of Dr. Joachim Scheven.
LACM. Natural History Museum of Los Angeles County. Courtesy of Mr. Roy R. Snelling.
MHNG. Muséum d'Histoire Naturelle, Geneva. Courtesy of Dr. Ivan Löbl.
MNHN. Muséum National d'Histoire Naturelle, Paris. Courtesy of Dr. Janine Casevitz-Weulersse.
MCSN. Museo Civico di Storia Naturale "Giacomo Doria", Genoa. Courtesy of Dr. Valter Raineri.
MCZC. Museum of Comparative Zoology, Harvard University, Cambridge, Mass. Courtesy of Mr. Stefan Cover.
MPEG. Museu Paraense Emílio Goeldi, Belém (Pará), Brazil. Courtesy of Dr. Ana Y. Harada.
MZSP. Museu de Zoologia, Universidade de São Paulo. Courtesy of Prof. Carlos Roberto Ferreira Brandão.
NHMB. Naturhistorisches Museum Basel. Courtesy of Dr. Michel Brancucci.
NHMW. Naturhistorisches Museum Wien. Courtesy of Dr. R. Contreras-Lichtenberg.
NHRS. Naturhistoriska Riksmuseet, Stockholm. Courtesy of Mr. Bert Gustafsson.
OXUM. Hope Entomological Collections, University of Oxford. Courtesy of Dr. Stephen J. Simpson and Mr. Christopher O'Toole.
USNM. United States Department of Agriculture, Agricultural Research Service, Systematic Entomology Laboratory, c/o National Museum of Natural History, Washington, D. C. Courtesy of Dr. David R. Smith.
ZMUC. Universitetets Zoologiske Museum, Copenhagen. Courtesy of Dr. Borge Petersen.
ZSMC. Zoologische Staatssammlung München. Courtesy of Mr. Erich Diller.

For some simple behavioural laboratory observations on the function of the soldiers we used what should have been a very large fragment (since it contained ca. 2,400 adult workers and soldiers and several pre-imaginal stages but no queen) of a colony of *Z. pusillus* from Botucatu (S. Paulo, Brazil), another much smaller colony of *Z. targionii* from Lins (S. Paulo, Brazil), and a nearly complete colony of *Z. angustus* from Botucatu (S. Paulo, Brazil). *Z. pusillus* should exemplify the species with soldiers without specialised cephalic morphology and the other two species should represent those with soldiers morphologically specialised to close the nest entrance with the head.

The biometry of caste and intra-castal polymorphism have been studied on four species selected so as to represent the major morphological trends we recognise. These species and the corresponding representative material we studied are the following:

Zacryptocerus auricomus (WHEELER), 128 workers (randomly selected among many more available) and 24 gynes from a single colony collected near Puerto Plata (Dominican Republic).

Cephalotes atratus (L.), 123 workers from the same colony from Lins (S. Paulo, Brazil) and 42 gynes from different localities (most of them in Amazonas, Brazil).

Zacryptocerus pusillus (KLUG), a random sample of 145 workers and 40 soldiers from a single colony collected in Botucatu (S. Paulo, Brazil) and 61 gynes from the same locality but from another colony.

Zacryptocerus angustus (MAYR), a random sample of 62 workers, 61 soldiers and all available 38 gynes from the same colony collected in Botucatu (S. Paulo, Brazil).

3. Terminology

For the reproductive female caste we use the term g y n e , already introduced by WHEELER (1908) and used consistently by BRIAN (1983) but reluctantly accepted by ant taxonomists, until now. This caste in most ant literature is generally termed "female", a sex and not a caste name which does not distinguish reproductive females from workers, of course. The term "queen", as used in some papers, is also inappropriate since not all gynes are queens. This distinction had already been made clear in the bee literature by MICHENER (1974) and introduced in the ant literature by WHEELER (1986).

The recent ant literature shows an increasing tendency to call the two neuter castes of various ant genera "minor workers" and "major workers". Papers of the early fifties started reporting the classic word "soldier" in parentheses after "major worker" and, later, the latter term expanded to substitute entirely for the former. The origin of this prejudice against the use of "soldier" appears to be a statement by WILSON (1953) where soldiers are described as one of the two "subcastes" of workers, i. e. "minor" and "major".

We shall call the larger Cephalotini neuters s o l d i e r s – as KEMPF did in most of his papers devoted to these ants – since this expression is less anthropomorphic than, e. g., another widely used term, "queen", and more exact. In addition, this is the name which has been specifically proposed for this caste and nobody ever suggested a valid reason to change it. In the literature there is abundant evidence (WILSON, 1976 b; COLE, 1980, 1983 b) that the so-called "major workers" of Cephalotini actually never work and in this paper (chapter 6.4.2) we shall show that some 18–35% of the members of this caste, under standard laboratory conditions, are permanently devoted to guarding the nest entrance, a function in perfect agreement with the romantic name of soldier. The Cephalotini "minor workers", in this paper, will be called simply w o r k e r s as the non-reproductive caste of ants is commonly called in absence of morphologically specialised soldiers. Workers and soldiers are the two neuter female castes, as opposed to the gyne (i. e. the reproductive) female caste. BARONI URBANI & PASSERA (1996) and BARONI URBANI (1998) showed that workers and true soldiers (i. e. not considering as soldiers large workers of polymorphic species) are produced from gynes in a parallel way, independent from each other; from this, it follows that both categories of individuals should be called castes since the term subcaste, implying a subset of a unique group, would be improper. The caste nomenclature we propose here, i. e. with a reproductive female caste opposed to two separate, non-reproductive, neuter female castes, i. e. workers and sol-

diers, is considerably different from that used in most current myrmecological literature.

It is nonetheless not original. The same caste nomenclature adopted in this paper had been already used by DARWIN (1859, Chapter 8) who wrote: "The castes, moreover, do not generally graduate into each other, but are perfectly well defined; being as distinct from each other, as are any two species of the same genus, or rather as any two genera of the same family. Thus in *Eciton*, there are working and soldier neuters, with jaws and instincts extraordinarily different". A correct, exhaustive definition of ant castes, similar to the one we use in this paper, has been already given by ANDRÉ (1888: 41–43) who adds that the terms major and minor worker should be restricted to the species in which frequent transitional forms between the two are known. We will follow this recommendation. Minor and major workers, in this sense, in *Cephalotes* are present only in *C. atratus* and, perhaps, in a few other insufficiently known members of its clade.

The name "soldier" referring to an ant caste, to our knowledge, has been introduced by HEER (1852) who, while dealing with *Pheidole megacephala*, wrote: "Die Großköpfe... dienen theilweise zur Vertheidigung der Wohnung, daher wir sie durch den Namen der S o l d a t e n vor den übrigen auszeichnen wollen". The term was immediately adopted, for example, by GUSTAV L. MAYR (1830 – 1908), by CARLO EMERY (1848 – 1925), by AUGUSTE FOREL (1848 – 1931), and by WILLIAM M. WHEELER (1865 – 1937) who used it in all their papers on ants, but never by FREDERICK SMITH (1805 – 1879) who firmly preferred the term "worker major".

The oldest mention of the term "worker" referred to ants we have been able to trace is in SWAMMERDAM (1737), who, since he never saw a soldier, did not separate soldiers from workers. The generic term "neuter" referable to both workers and soldiers appears to have been used for the first time by OLIVIER (1791).

We recognise, hence, three different female castes and two comprehensive terms for members thereof among ants. We recommend their identification by means of the names listed below and briefly defined as follows:

F e m a l e . A sex and not a caste name. Three female castes (gyne, worker and soldier) are known so far in ants.

G y n e (WHEELER, 1908). A female caste devoted primarily to reproduction.

N e u t e r (OLIVIER, 1791; DARWIN, 1859). Comprehensive term for both primarily non-reproductive female castes, i. e. workers and soldiers.

W o r k e r (SWAMMERDAM, 1737). One of the two neuter discrete castes and often the unique neuter caste. When both neuter castes are present, workers are the most gyne-dissimilar neuters. Workers may be polymorphic. In this case the largest, middle and smallest individuals are often called with the English (and Latin) adjectives major, (*media*), and minor worker (ANDRÉ, 1888). If the Latin adjectives are used consequently, the plural for the three subcastes is workers (= *formicae operariae*) *majores*, *mediae*, and *minores*.

S o l d i e r (HEER, 1852). The second neuter discrete caste. Soldiers do not exist in absence of workers. They are regularly more similar to gynes than are workers and often exhibit peculiar morphological adaptations for defence.

In the specific descriptions we used the following measurements and indices, defined and listed below with their relative abbreviations. Our decision to include spines and lamellae in measuring widths is destined to include a broader spectrum of individual variability in our results. This course of action has been dictated by the

difficulty to define in a precise way the border of some body parts when it bears one or another type of integumental expansions.

HL = Head length measured dorsally on the sagittal plane.
HW = Maximum head width behind the eyes, including the vertexal spines and/or lamellae, if present.
PW = Maximum pronotum width in dorsal view including the propodeal spines, apodemes, and lamellae, if present.
PeW = Maximum petiole width in dorsal view, including spines or lamellae, if present.
PpW = Maximum postpetiole width in dorsal view, including spines or lamellae, if present.
HBaL = Maximum length of the hind basitarsus.
HBaW = Maximum width of the hind basitarsus.
CI (Cephalic Index) = HWx100/HL.
PI (Pronotal Index) = HWx100/PW.
PPeI (Petiolar Index) = PWx100/PeW.
PPpI (Petiole and Postpetiole Index) = PWx100/PpW.
HBaI (Hind Basitarsal Index) = HBaWx100/HBaL.

Vertex and vertexal margin are defined as the dorsal area and the posterior margin of the head in prognathous position as seen in dorsal view. These terms are used in preference to the obsolete, and incorrect, "occiput" and "occipital margin" in agreement with the morphological nomenclature of other Hymenoptera. This need for uniformity in ant literature has been already stressed by SNELLING (1995).

In the species descriptions we shall often refer to membranaceous borders and appendages, a terminology already established in previous papers on the Cephalotini. It should be clear, however, that these body parts have a membranaceous aspect but share no other characteristic with true membranes.

Scapular angle (a term already introduced by KEMPF) is defined here as the characteristic cephalotine laterally angulate anterior pronotal border passing without continuity, i. e. with an angle, into the propleurae.

4. Methods

4.1. Preparation and study of specimens

Most amber specimens have been cut and re-polished to improve observation of the ants and to separate the Cephalotini from other inclusions. The description of the amber specimens and the list of non-cephalotine inclusions in the amber samples we gave in chapter 2 of this paper refer to the original status of the sample, as it was before our preparation. All amber removed – with or without inclusions – is kept in the same collection as the fossil cephalotine specimens and can be identified by means of their relative collection accession numbers as indicated in chapter 2.

All measurements and drawings of amber specimens have been made in 66% sucrose solution to reduce optical deformation of the specimen.

Male genitalia of extant species were dissected in water, cleaned in 5% KOH solution and mounted on microscopic slides in Euparal. Whenever possible, at least two genital apparatuses per species were examined and often more. Since no significant variability was observed, the drawings are based on one specimen only. Because of their reduced size the genitalia and the subgenital plate were first sketched under a stereomicroscope in order to properly understand their plastic appearance and the

spatial relationships between the parts. The final drawings were always executed by means of a compound microscope to attain a higher degree of precision.

All ink drawings are due to the talent and to the patience of Armin Coray.

4.2. Phylogenetic analyses and reconstructions

For the species-level analysis we coded as separate binary characters some characters which could have been considered as unique multistate characters. The reasons for our course of action are twofold: (1) since these characters seem to have simple, apparently equivalent, adaptive value, we did not dare attribute to them *a priori* an evolutionary direction; and, (2) if we had coded these characters as being unordered multistate, the unique sharing of a character state by the members of a clade may not appear synapomorphic in the cladistic analysis since often, in an unordered multistate sequence, the ancestral state can not be determined. In our binary recoding of characters we systematically applied nonadditive coding to avoid excessive weighting of the characters in question.

In performing the species-level analyses we faced another problem appearing frequently in earlier phylogenetic studies of the Formicidae and previously unresolved: the separate use of the same or of obviously homologous character(s) for different sexes or castes. If, on the one hand, the same character must be coded differently among different sexes or castes when it contains potentially useful information, on the other hand it will result overweighed when it is caste or sex invariant. In previous studies these characters have been treated as the other characters, i. e. they have been overweighed. To avoid this drawback we used a "standard weight" for all non-homologous characters. This weight, to be attributed to all characters appearing only once in the data matrix, is equal to the maximum number of times that the same or a homologous character is repeated in the same matrix. All homologous characters have been weighted by a fraction of the "standard weight" equal to their own frequency of presence in the data matrix. We had only a limited number of such repeated characters which we used at most twice in our species-level analysis of the Cephalotini. Most characters, hence, have been weighted 2 and all those scored twice among workers and soldiers or among soldiers and gynes have been weighted 1.

The cladistic analyses were performed by means of the software PAUP 3.1.1 (SWOFFORD, 1993). Search for the shortest tree(s) for our data matrices was by means of the exact "branch-and-bound" method (HENDY & PENNY, 1982) on the genus-level matrix and, due to the great number of taxa involved, by the mathematically approximate, heuristic methods implemented in PAUP for the species-level analysis. Given the size and the numerical complexity of our species matrix, we explored all combinations of the three most promising methods of stepwise addition of taxa (closest, "simple", and random) and of the three methods of branch swapping (nearest neighbour interchanges, subtree pruning-regrafting, and tree bisection-reconnection) implemented in PAUP.

All our searches were performed with the following options: MULPARS (allowing the saving all most parsimonious trees), KEEP (minimal trees only) and HOLD = 100 to reduce the risk of remaining trapped in a local optimum. The latter option, of course, was ignored during the random addition of taxa.

On the contrary, the following options have been constantly deactivated in every search: COLLAPSE and STEEPEST DESCENT. The reasons for their exclusion are those already explained by SWOFFORD (1993) in the PAUP user's manual.

All searches were performed on a Macintosh Quadra 950 with 38 MB free RAM memory and with a MAXTREES limit of 10,000, i. e. nearly the maximum number of trees with 135 terminal branches that this computer configuration can afford without significantly slowing down the search.

To obtain a statistical appreciation of the reliability of the results of our cladistic analyses we performed the following tests:

1. Comparison of our shortest tree with the length of 10,000 randomly generated trees with the same number of terminal branches (FITCH, 1979; HUELSENBECK, 1991). This test is implemented in PAUP 3.1.1.

2. A permutation tail probability test according to FAITH & CRANSTON (1991). To perform this test 99 matrices containing the same number and quality of character states as our data matrix but randomly permuted were generated by means of the Pascal program César written by Véronique Perrot. Each permuted data matrix was searched for the shortest tree(s) by PAUP by means of simple addition of taxa, branch swapping by tree bisection-reconnection, and with a MAXTREES limit of 100.

3. We also attempted a bootstrap analysis of our species level data matrix. Given the high number of taxa included in our analysis (135), any attempt to completely bootstrap the data matrix would end in a memory overflow due to the great number of trees retained and/or in tremendous computing times. To overcome this inconvenience we performed a great number of bootstrap replicates (10,000) by random addition of taxa and swapping branches by subtree pruning-regrafting, i. e. by means of the two searching algorithms which, a posteriori, resulted most efficient on our data matrix. To avoid memory overflow, only one tree was retained at each replicate. In this way the maximum number of trees to be retained in memory would not exceed 10,000. Our hope was that the high number of bootstrap replicates could compensate, at least in part, for the low number of (suboptimal) trees retained.

Some graphic display and character analysis has been obtained by means of MacClade 3 (MADDISON & MADDISON, 1992), version 05.

4.3. Histology and structure of the proventriculus

Histological preparations of the proventriculus were obtained from entire *Z. pusillus* workers or from freshly dissected proventriculi of *H. auricomus* and *Z. clypeatus* fixed in Bouin and in Heidenhain's "Susa", or in 6% glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.3) for 90' at 4° C. The Bouin and "Susa" fixed proventriculi were stored in 80% alcohol, embedded in paraffin, and serially cut in 7 – 10 µm thick sections. The sections were stained with hematoxyline, Mayer's eosin, alcian blue, Azan, and PAS (see e. g. BURCK, 1973). Those fixed in glutaraldehyde were embedded in Spurr and in Epon 812 and partly cut in semi-thin sections of 240 – 190 nm for phase contrast examination.

SEM examination of freshly killed tissues to describe the internal proventricular morphology was obtained by fixation of fragments of the intestine of the ants immediately after dissection in 6% glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.3) for 90' at 4° C. Afterwards the fragments were washed three times in 0.2 M Na-cacodylate buffer with 13.6% sucrose and left in the same medium overnight at 4° C. The following day the fragments were transferred to 2% osmium with 0.2 M Na-cacodylate buffer for two hours at 4° C. Dehydration was by transfer for 10 minutes

each in seven progressive baths of acetone ranging from 30% to 100%; the last acetone dehydration being repeated twice. The specimens were thereafter partly dried to the critical point, glued to aluminium specimens-holders, and gold coated as standard for SEM examination.

4.4. Description of caste polymorphism

The traditional biometric approach to caste description has lost part of its significance since demonstrations of allometry formerly interpreted as a proof of the existence of subcastes within a unique worker caste, have been often shown to refer to ontogenetically different, not comparable, castes (Baroni Urbani & Passera, 1996). Stated otherwise, demonstration of allometry among workers can not be interpreted as a case of incipient soldier formation. Intra-caste biometry has still been studied in this paper as a potential tool for comparisons of the same caste between species.

In addition to the conventional biometric caste description, the possibilities of a grid transformation method have been also explored in this paper. Grid transformation methods were introduced by D'Arcy Thompson (1917). For the ant literature, previous examples can be found in Baroni Urbani (1974) and Franks & Norris (1987). These methods have seldom been used until now for at least two different reasons: 1) the great time investment required, and, 2) the exact course between two fixed points of the transformed lines constituting a grid remains rather arbitrary. Here we have attempted to devise a standard method based on available computer software, a facility which should greatly reduce both time and subjectivity.

4.4.1. The biometric approach

In order to describe intra-caste polymorphism biometrically, two standard measurements were made for all species and castes investigated: the maximum pronotal width in dorsal view (pronotal spines included), and the maximum hind tibia length measured on its external surface. Whenever possible, measurements were performed either on all specimens available for a species or on a random sample of ants from the same colony. All the workers and the soldiers of every species studied originate regularly from one single nest. In only one instance were a sufficient number of gynes available from the same colony. In other cases we measured gynes from the same locality as the neuter colony or from other localities as close as possible to it. This means that, in these cases, together with the intra-colonial variability, we also measured some inter-colonial and some geographic variability. The latter two sources of variation are not likely to affect the aims of our analysis, i. e. intra-caste biometry in a significant way. In order to detect possible cases of allometric growth, as suggested by van Boven (1970), we concentrated on the variation of pronotal width (a highly variable body part among Cephalotini) as compared with hind tibia length (a relatively invariant character). While the results of our study on the one hand confirm the correctness of our choice, on the other hand, this approach reduces the possibility of comparing our results with other findings already available from the literature in which other body parts were considered.

In this paper we tested the descriptive power of the following set of different models on each caste we measured:

1. Simple regression of the untransformed data.
2. Simple regression of log-transformed data.
3. Polynomial regression of untransformed data with polynomials of increasing degree.

The decision about the best fitting model was made by comparing the adjusted R^2 for every model (for a simple explanation of the meaning of the adjusted R^2, see the Abacus Concepts Manual, StatView, 1992). A complex model was considered superior to a simpler one only when its adjusted R^2 corresponds to an explanatory power greater than an arbitrarily fixed value of 5%.

4.4.2. The grid transformation approach

SEM pictures of complete (i. e. including legs and antennae) ants were used as the starting material for the analyses. Even very well mounted ants, however, show inequalities in body position and orientation which are destined to adversely affect their symmetry under SEM magnification. For this reason, the ants of the original pictures were digitally "re-mounted" in a standard position against a perfectly white background using Adobe Photoshop™ 3.05 (Knoll et al., 1995). For each caste analysis we considered the gyne as the most undifferentiated caste and constructed a square grid with squares of sides measuring exactly 1/4 of the maximum head width of the gyne. The grid was extended so to cover the whole ant body. To standardise its position the grid was placed so that the longitudinal body axis of the ant and a reference transverse line (called x_0) were adjusted to intersect over the centre of the anterior border of the head. In this way we obtained symmetrical left (y_{-1}, y_{-2},... y_{-n}) and right (y_1, y_2,... y_n) lines covering the whole ant body. The horizontal lines are essentially negative since they are drawn under to the x_0 one (x_{-1}, x_{-2}, ... x_{-n}); positive horizontal lines (x_1, x_2) are less important and are needed only to encompass the parts of the antennae and the mandibles extending in front of the anterior clypeal border.

The gyne morphology was transformed digitally into the soldier or worker morphology by means of Morph™ 2.01 (Maxwell, 1993). When we judged the transformation satisfactory we substituted the image of the gyne with its corresponding grid. In this way we obtained a computed grid transformation corresponding to the caste-dependant somatic modifications of the analysed caste. Unfortunately, Morph™ also transforms accordingly the thickness of the lines of the grid. The "morphed" grid lines have been re-drawn in the original thickness and the coordinates of all intersection points between the transformed *x* and *y* axes have been measured by means of NIH Image 1.60 (Rasbond, 1996). The grids obtained from transformation of workers and, when present, of soldiers of different species have been compared by Kaiser's image analysis. We used the coordinates of the intersection points as inputs for the successive analyses performing orthotran and varimax transformations of the initial factor solution. Comparison of the deformation among homologous coordinates should allow a precise localisation of the caste-dependant somatic modifications and their description and measure. It is obvious that different degrees of accuracy can be obtained with grids of different size. We consider the results presented in this paper as essentially exploratory and both their significance and their value can be better appraised when the results of further analyses on other ant genera will be available.

4.5. Behaviour of the soldiers

Laboratory observations on the function of cephalotine soldiers have been carried out largely on two colonies, one of *Z. pusillus* and one of *Z. angustus*. We hosted each experimental colony in a slightly modified Janet nest connected by a short Plexiglas pipe to a foraging arena. The Plexiglas pipe was cut longitudinally in two in part and the two halves were fixed along only one edge by a piece of scotch tape so that they could be opened allowing access to the ants inside. The ants were transferred to the arena along with fragments of the hollow tree twigs from their original nest. They entered the artificial nest spontaneously, foraged in the arena and concentrated several individuals in and around the connecting pipe as we already observed in the entrances of nests of these ants under natural conditions. The observations consisted of counting separately the number of soldiers and workers staying in or immediately outside (i. e. not simply walking around or passing through) the Plexiglas pipe at time intervals > 2 hours. In comparing the results we obtained from these two nests, we must mention a difference in the experimental conditions of the two colonies which may have affected our results to some extent: both nests were connected to the foraging arena by a Plexiglas pipe of 10 mm internal diameter, i. e. ca. 6 times larger than the average pronotal width of the *pusillus* soldiers and ca. 5 times larger than the average pronotal width of the *angustus* soldiers. This difference may affect the total number of soldiers potentially devoted to the entrance blocking function. For this reason we do not attribute much value to the actual number of soldiers we recorded in the nest entrance during our observations, and we claim that the numbers of soldiers or workers devoted to this function reflect the behaviour of these species under natural conditions. The latter is likely to vary from nest to nest according to the number, the size, and the shape, of the nest entrance(s). To take just one example, the natural nest from which our *angustus* colony originated had ca. 10 different entrances, the largest of which measured 7x8 mm. It is clear that our estimates of the number of individuals watching the nest entrance are underestimated compared with several natural situations.

Our aim was simply to investigate potential differences among soldiers and workers involved in entrance watching under standard conditions for two species showing different degrees of morphological adaptation to this task.

Since each individual observation represents a test of our hypothesis regarding a numerically different participation of the two castes in the "entrance watching function", application of a conventional statistical test to each observation is possible, but would make interpretation of the results difficult. To avoid the problem of multiple testing, the following procedure (suggested and computed by Paul Jordan to whom we are indebted) was followed:

1. The original data have been transformed into logarithms.
2. The odds-ratio has been computed on the transformed data as $n_1/(N_w-n_1)/\ n_2/(N_s-\ n_2)$, where n_1 and n_2 are respectively the numbers of workers and of soldiers recorded at each observation time and N_w and N_s are the total number of workers and of soldiers in the nest at the time in which the observations were conducted.
3. This model estimates the mean log (odds-ratio) as the intercept. The mean value is $e^{(\mu+s/2)}$.
4. A decomposition of variance into variance between days, and variance within days, was performed by means of a variance component analysis.

At each count the soldiers in or around the nest entrance were marked by means of a small drop of nail polish on the mesosoma or on the gaster. In this way we obtained a measure of the number of soldiers possibly devoted to an "entrance guarding" function and of their individual fidelity to this task. Application of the nail polish did not affect the individual's behaviour in any visible way and the marking lasted several weeks.

Our observations continued until we encountered only marked ants among the individuals devoted to the "entrance guarding" function. These marked ants were considered as a behaviourally specialised set of individuals devoted primarily to the "entrance guarding" function. Finally, we tested the hypothesis that our result could be due to chance alone by means of the hypergeometric distribution. In this model the probability p of encountering k marked individuals at each observation is given by the formula

$$p = \frac{\binom{K}{k}\binom{N-K}{n-k}}{\binom{N}{n}}$$

N = total number of individuals
K = number of marked individuals
$N-K$ = number of unmarked individuals
n = number of individuals guarding the nest entrance in a given observation
k = number of marked individuals guarding the nest entrance in a given observation
$n-k$ = number of unmarked individuals guarding the nest entrance in a given observation.

5. Taxonomic results

5.1. The tribe Cephalotini: limits, definition and constituent genera

The taxonomic knowledge of the Cephalotini is quite good and reliable. This fact, relatively rare for a group of tropical ants, is due practically to the efforts of a single man, the late WALTER W. KEMPF who, in an important series of very accurate papers (1949 – 1974) contributed in a significant way to most of what we know and we understand about these ants today. We are not willing to re-trace here the oldest history of classification and of nomenclature of these ants. For those interested in it, at the appropriate places in this paper, we shall make reference to the pertinent papers by KEMPF whose acquisitions we generally regard as a reasonable certainty and we shall start our analysis from them. Most of the changes to his classification we will introduce in this paper are the straightforward result of examining type material not available to KEMPF who did virtually all his research work geographically isolated from the most important entomological collections.

In his first comprehensive revisionary work on Cephalotini, KEMPF (1951) recognised the following six valid genera: *Procryptocerus*, *Cephalotes*, *Eucryptocerus*, *Zacryptocerus*, *Hypocryptocerus*, and *Paracryptocerus*. The validity of these genera remained unquestioned until BROWN (1973) suggested that the tribe Cephalotini should contain only two valid genera: *Cephalotes* and *Procryptocerus*. This provoked a prompt reaction by KEMPF (1973) who accepted (and justified) the synonymies of *Paracryptocerus* EMERY and *Hypocryptocerus* WHEELER with *Zacryptocerus*

WHEELER but listed a set of characters distinguishing the remaining four genera, namely *Cephalotes*, *Procryptocerus*, *Eucryptocerus*, and *Zacryptocerus*. Later on, *Hypocryptocerus* and *Paracryptocerus* have been considered repeatedly as good genera only by WILSON (1985 a, 1985 b and 1988) who did not add reasons to justify his point of view. The characters used by KEMPF (l. c.) to separate the four cephalotine genera appeared significant and invariant within each genus but they are differently distributed within the genera in different combinations, i. e. no attempt was made to distinguish between plesiomorphies and apomorphies (for understandable reasons considering that KEMPF's paper was published in 1973). KEMPF also presented an operational key to the identification of the four genera on the basis of these characters. For these reasons the generic classification proposed by KEMPF (1973) remained practically unquestioned until today and the characters used to separate these genera in his key have been re-used in subsequent keys for the neotropical genera of ants by BARONI URBANI (1983), HÖLLDOBLER & WILSON (1990) and BOLTON (1994). The approach taken in the recent book by JAFFE (1993) is less clear since the traditional genera recognised by KEMPF (1973), i. e. *Procryptocerus*, *Cephalotes*, *Eucryptocerus*, and *Zacryptocerus*, are listed as members of the Cephalotini, but *Eucryptocerus* is omitted from the accompanying key to the genera (written by John LATTKE) and probably included in *Cephalotes*.

Finally, VIERBERGEN & SCHEVEN (1995) described a new genus of Cephalotini from Dominican amber: *Exocryptocerus*. The new genus is admitted to show "the characters given for the worker of the tribe Cephalotini by Kempf (1951)... except the articulation of the postpetiole, which can be absent". Despite examining all the material on which this genus is based we have been unable to recognise or understand this character. The paper does not specify which articulation (i. e. that with the petiole or that with the gaster) should be missing, and all the specimens we studied and even the figures accompanying the description of the new genus show both articulations. We will propose the synonymy of this genus under the generic treatment in chapter 5.2.

Partly unpublished Recent and fossil material available for the present study revealed that the three most important characters used by KEMPF (l. c.) to separate the genera *Eucryptocerus* and *Zacryptocerus*, i. e. the globose eyes and the pedicel dorsally unarmed for the first, and the petiole with lateral expansions for the second, do not apply to all species of the two genera.

In fact, among the Recent species, globose eyes very similar to those of *Eucryptocerus* can be found among species of both genera, *Cephalotes* (i. e. *alfaroi* and *serraticeps*) and *Zacryptocerus* (i. e. *bruchi* and *minutus*). Some amber species unknown to KEMPF (e. g. *jansei* and *bloosi*, see Figs. 246 and 258) converge even more with the *Eucryptocerus* ocular morphology, though exhibiting a "typical *Zacryptocerus*" habitus.

Traditionally, a dorsally bispinose petiole should be a synapomorphic character of *Cephalotes*, though the spines may be individually reduced to short denticles or absent (e. g. in *C. atratus* (L.)). A perfectly comparable condition can be observed in *Zacryptocerus targionii* (EMERY), though KEMPF apparently never doubted that this should weaken in a significant way the value of this character in defining *Cephalotes*. A similar morphology is to be found in *Zacryptocerus adolphi* (EMERY). The presence of such spines is not mentioned in the original description of *adolphi* by EMERY (1905), nor in the re-description of the species by KEMPF (1960), although the

spines are drawn in Fig. 20 of the latter paper; the spines, of course, are clearly visible in all the specimens we have been able to examine during the present study.

Analogously, unpublished material of *Z. solidus* and *Z. pusillus* contains smaller individuals with practically unarmed petiolar nodes and the Dominican amber species *jansei* is completely devoid of spines and expansions on the petiolar nodes.

Two of these three characters are therefore polymorphic and presumably not autapomorphic in the taxa they are supposed to characterise; the third (absence of petiolar spines) remains consistent within *Eucryptocerus* but is equally present among its most closely related taxa.

For the reasons above we attempted a cladistic placement of the four Cephalotini genera recognised by KEMPF, although the results of our analysis are partly predictable since we did not consider three formerly important characters: the "globose eyes" (presumed apomorphy of *Eucryptocerus*), the "absence of dorsal petiolar spines" (presumed apomorphy of *Eucryptocerus*), and the "laterally armed petiole" (presumed apomorphy of *Zacryptocerus*) just discussed.

Given the arguments concerning insecurity among generic relationships and the tribal limits already mentioned in the introduction to the "true" genera of Cephalotini, in the analysis, we added also the Old World genus *Cataulacus*. For the outgroup comparison we used the genera: *Myrmecina* as suggested by EMERY (1920), and *Pheidole* as suggested by KUGLER (1978).

There is at least one such potential sister group of the Cephalotini which we did not include in our data matrix: the Attini. The two tribes share at least the following important characters: expanded frontal carinae, 11-jointed antennae, heavily armoured integument with spines and protuberances, loss of the stinging capacity with consequent morphological reduction of the sting (including unimodal sensillar pattern on the gonostyli), exclusively Neotropical distribution, and largely vegetarian diet (this character for the Cephalotini will be demonstrated later in this paper). To this list one might also add similarities in the morphology of the proventriculus as described by DEMOSS (1973) and discussed below under character # 20. We did not include the Attini in our cladistic analysis because the literature suggests that the similarities in proventricular morphology mainly concern the genus *Trachymyrmex* rather than the other Attini genera and we do not have sufficient fresh Attini material to verify these possibilities. Such a situation (i. e. a greater similarity of the Cephalotini to *Trachymyrmex* than to other attine genera) is very unlikely and could result, among other things, in a paraphyly of the tribe Attini.

Except for the three characters discussed above, we included in our data matrix as potential synapomorphies all genus-level and tribe-level Cephalotini characters resulting from the literature; we also included the numerous characters derived from the sting morphology as described by KUGLER (1978) (characters 24 – 49 of our list are taken entirely from his paper), and a few more we found during the present study.

WHEELER (1984) previously attempted a cladistic analysis of the relationships among three cephalotine genera based on six behavioural characters. Although it appears plausible that these characters should have generic value, as WHEELER herself (l. c.) admits, the main potential source of error in such an analysis stems from the fact that the behaviours considered have been only observed in one species per genus. We concur with this scepticism. However, since some of the internal morphological characters used to infer phylogenetic conclusions often are extrapolated from

samples of comparable size, we thought it fair to warn again of the potential weakness of these characters while including them in our analysis. We excluded only one of the behavioural characters considered by WHEELER (1984) from the analysis, namely the production of "infrabuccal pellets". Presence or absence of this behaviour among the Cephalotini in WHEELER (l. c.) had been coded in part after CORN (1976) who states (page 169) that no "consumption" of pellets had been observed in *Cephalotes*. We observed the production of pellets by *C. atratus* in our laboratory (see later, Chapter 6.3.3). This character, hence, is cladistically uninformative since it is present in *Cephalotes*, *Zacryptocerus* and *Procryptocerus*, and unknown in all other taxa considered.

The following is a list and description of the characters we considered of potential synapomorphic value:

1. Sexual dimorphism pronounced (0), or reduced, i. e. with males similar to gynes and workers (1). Important secondary sexual characters of males are almost universal among ants. They often include a remarkable reduction in size or at least a reduction of the cephalic capsule (compared with the female morphology) accompanied by a proportional increase in size of the eyes, of the antennae, of the legs and of the wings. Apart from the obvious differences due to the possession of wings and the accompanying mesosomal sclerites *Cataulacus* is remarkable in this respect in having worker-like males.

2. Male. Size equal to or smaller than the gyne (0), or larger than the gyne (1).

3. Worker (and gyne). Border of the oral cavity ventrally straight (0), or deeply concave (1).

4. Worker and gyne. Eye position: behind the antennal scrobe (0), below the antennal scrobe (1), or above the antennal scrobe (2). In fact the eyes of the three species formerly included in *Zacryptocerus* s. str. (*clypeatus*, *ustus* and *membranaceus*) are over the antennal scrobes but they originate from a peduncle clearly positioned behind the scrobes. For this reason, the current genus *Zacryptocerus* s. l. has been uniformly coded as "0" for this character.

5. Worker and gyne. Antennal scrobes short, not reaching the posterior border of the eyes (0), or long, surpassing the posterior border of the eyes (1).

6. Worker and gyne. Frontal carinae reduced, not covering the genae (0), or broadly expanded, covering at least most of the genae (1).

7. Worker and gyne . Antennal scape reaching or surpassing the vertexal border (0), or not reaching the vertexal border (1).

8. Male. Antennal scape much shorter than five times the first funicular joint (0), or much longer than five times the first funicular joint (1).

9. Worker and gyne. Vertexal angles rounded (0), or dentate or spinose (1).

10. Worker and gyne. Antennae 12-jointed (0), 11-jointed (1), or 10-jointed (2).

11. Male. Antennae 13-jointed (0), or 11-jointed (1).

12. Worker and gyne. Mandibles continuously decreasing in thickness from the articulation to the apex (0), or with a very thick basal part separated from the true mandibular blade by a strong depression on the internal side (1).

13. Male. Mandibles only gradually widening from the base to the apex (0), or broadly widening, ca. four times wider at the apex than at the base (1).

14. Worker (and gyne and male?). Maxillary palps short, not reaching the hypostomal bridge in relaxed position (0), or extending over the hypostomal bridge in relaxed position (1).

15. Worker (and gyne and male?). Palpal formula 5,3 (0), or 4,3 (1), or 3,2 or 2,2 (2).

16. Worker (and gyne?). Humeral angles rounded (0), or armed with spines or lamellae (1). State 1 of this character should be a classical synapomorphy for *Cephalotes*, *Eucryptocerus* and *Zacryptocerus* but its value appears slightly diminished by the fact that *Z. bimaculatus* and *varians* present a condition somewhat intermediate between the two extremes.

17. Worker and gyne. Petiole anteriorly pedunculate (0), or sessile (1).

18. Worker and gyne. Petiolar sternite short, not prolonged anteriorly between the metapleurae (0), or prolonged anteriorly between the metapleurae (1).

19. Worker and gyne. Fourth abdominal (first gastral) tergite at least 1/4 shorter than the mesosoma (0), or as long as the mesosoma or longer (1).

20. Worker and gyne. Stridulatory organ present (1), or absent (0). This is the morphological correlate of WHEELER's (1984) behavioural character "stridulate". We preferred to code presence or absence of the stridulatory organ rather than its use. Distribution of the organ among the taxa considered is given after MARKL (1973).

21. Worker. Integument generally thin and moderately hard, deformable by compression in relaxed specimens (0), or thick and much harder: pressure exerted on the cephalic capsule or on the mesosoma of relaxed specimens results in a break rather than in deformation (1).

22. Worker (and gyne and male?). Proventriculus normally shaped, elongate and without bulb (0), or in form of mushroom (1). State 1 of this character (Fig. 19) should be one of the strongest Cephalotini synapomorphies. Presence or absence of this structure among the taxa considered here has been coded essentially after FOREL (1878), EMERY (1888) , DEMOSS (1973) and CAETANO (1984). It should be noted that DEMOSS (1973) for *Trachymyrmex arizonensis* (Attini) reports, describes and figures a proventricular morphology very similar to the one of the Cephalotini. This contrasts in part with the mention of unspecialised proventriculi in *Atta* by FOREL (1878) and with the detailed description and illustration of the proventriculi of four *Atta* species by CAETANO (1984). The presentation of the results by DE MOSS (l. c.) is equivocal, since, first (p. 127) he states that "the morphology of the sieve of *T. arizonensis* is identical to that of *Cryptocerus texanus*", and later (p. 130) it is said that "the proventriculi of *A*[*tta*]. *texana* and *T. arizonensis* are morphologically more similar than are the proventriculi of any other two myrmicine genera examined". In a single paper CAETANO (1984) describes the proventricular morphology of four species of *Atta* and two species of *Cephalotes* (all different from those examined by DE MOSS, 1973) and emphasises their differences rather than their similarities. The fact remains that Fig. 23 B (proventriculus of *C. texanus*) and Fig. 25 B (proventriculus of *Trachymyrmex arizonensis*) in DE MOSS (1973) are identical. Dissections of proventriculi of *Trachymyrmex* spp. fixed in alcohol available for the present study failed to reveal any cuticular framework sufficiently sclerified to allow a clear separation from the rest of the intestine. For *Trachymyrmex* we have been unable to detect any kind of non-deformed structure in such material in contrast with the 100% successful dissections we performed on all alcohol preserved Cephalotini we examined. We therefore regard the presence of an easily recognisable sclerified cuticular framework as a sufficient indication for uniqueness of the Cephalotini among the whole Myrmicinae.

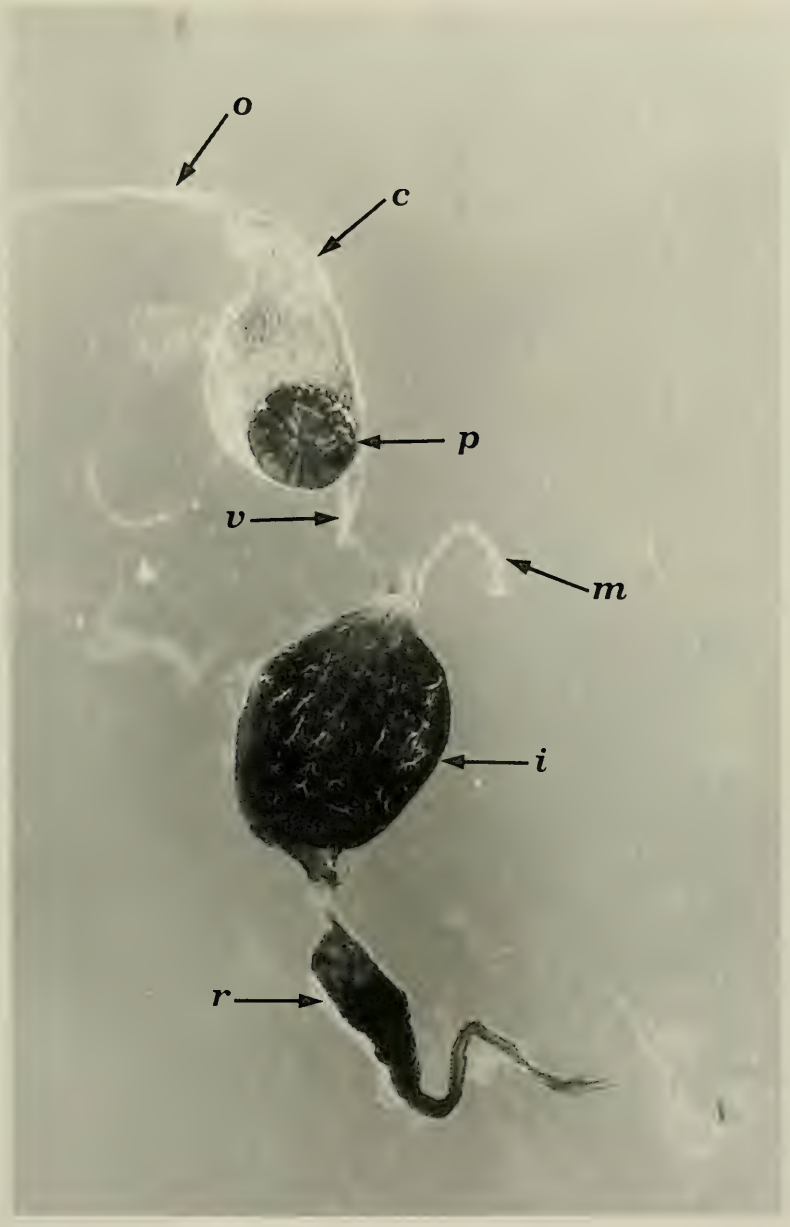


Fig. 19. *Cephalotes atratus* (LINNAEUS), worker, separate intestine: *o*, oesophagus, *c*, crop, *p*, proventriculus (visible in transparency through the crop), *v*, ventriculus, *m*, Malpighian tubulus, *i*, ileum, *r*, rectum. Two morphological traits of the alimentary canal are supposed to characterise the tribe Cephalotini: the septate mushroom-shaped proventriculus, a character unique among all Formicidae examined so far, and the hypertrophied ileum, a constitution shared only with the supposedly convergent Old World Cataulacini.

23. Worker and gyne (and male?). Ileum subequal in diameter throughout its length (0), or proximally thickened and filled with micro-organisms (1) (Fig. 19). Similarity of the ilean structure among Cephalotini and Cataulacini is coded here according to CAETANO & DA CRUZ LANDIM (1987) and CAETANO et al. (1994). Sharing of this character might represent a potential synapomorphy for the two tribes although the weight of this character in our analysis is weakened by the fact that the absence of the bacterial thickening in the ileum of the outgroups remains very probable but undemonstrated. The sole potential source of information about the state of this character in the outgroups (DE MOSS, 1973) does not mention it in the text and the accompanying figures are not very clear: they show normally thin ilea for both *Pheidole* and *Myrmecina*, but similarly, the thickening in *Zacryptocerus* is not very evident.

24. Gyne (and male?). Forewing with radial cell closed (0), or open (1).

25. Worker. Spiracular plate with ridge sclerotized only laterally (0), or completely sclerotized (1).

25. Worker. Anterior apodeme of the spiracular plate narrow (0), or wide (1).

27. Worker. Dorsal notch of the spiracular plate absent (0), or present (1).

28. Worker. Posteroventral corner of the spiracular plate absent or very reduced (0), or very elongate (1).

29. Worker. Posterodorsal lobe of the spiracular plate absent (0), or narrow but present (1).

30. Worker. Posterodorsal edge of the spiracular plate reduced to a membrane (0), or present as a distinct corner (1).

31. Worker. Quadrate plate two times or more, more narrow ventrally than dorsally (0), or of comparable width dorsally and ventrally (1).

32. Worker. Apodeme of the quadrate plate much smaller than the body of the plate (0), or much larger than the body of plate (1).

33. Worker. Posterior edge of the quadrate plate emarginate (0), or entire (1).

34. Worker. Anal plate membranous, without discernible edges (0), or partially defined (1).

35. Worker. Sensilla of the anal plate restricted to the margin (0), or extending to the dorsal surface (1).

36. Worker. Sensilla of the anal plate absent (0), trichoidea present (1), basiconica present (2).

37. Worker. Oblong plate without posterior apodeme (0), with short posterior apodeme (1), or with long posterior apodeme (2).

38. Worker. Subterminal tubercle of the oblong plate absent (0), or present (1).

39. Worker. Postincision of the oblong plate not extending around the dorsal end of the fulcral arm (0), present above the dorsal end of fulcral arm but not far anteriorly (1), or extending far anteriorly to the dorsal end of the fulcral arm (2).

40. Worker. Terminal sensilla of the gonostyli without terminal setae or chaetae (0), or with a dorsoterminal chaeta (1).

41. Worker. Gonostyli without (0), or with (1) sensilla basiconica.

42. Worker. Dorsal tubercle of the triangular plate absent (0), or reduced but present (1).

43. Worker. Median tubercle of the triangular plate absent (0), or present (1).

44. Worker. Distal half of the lancet with parallel (0), or convergent dorsal and ventral edges (1).

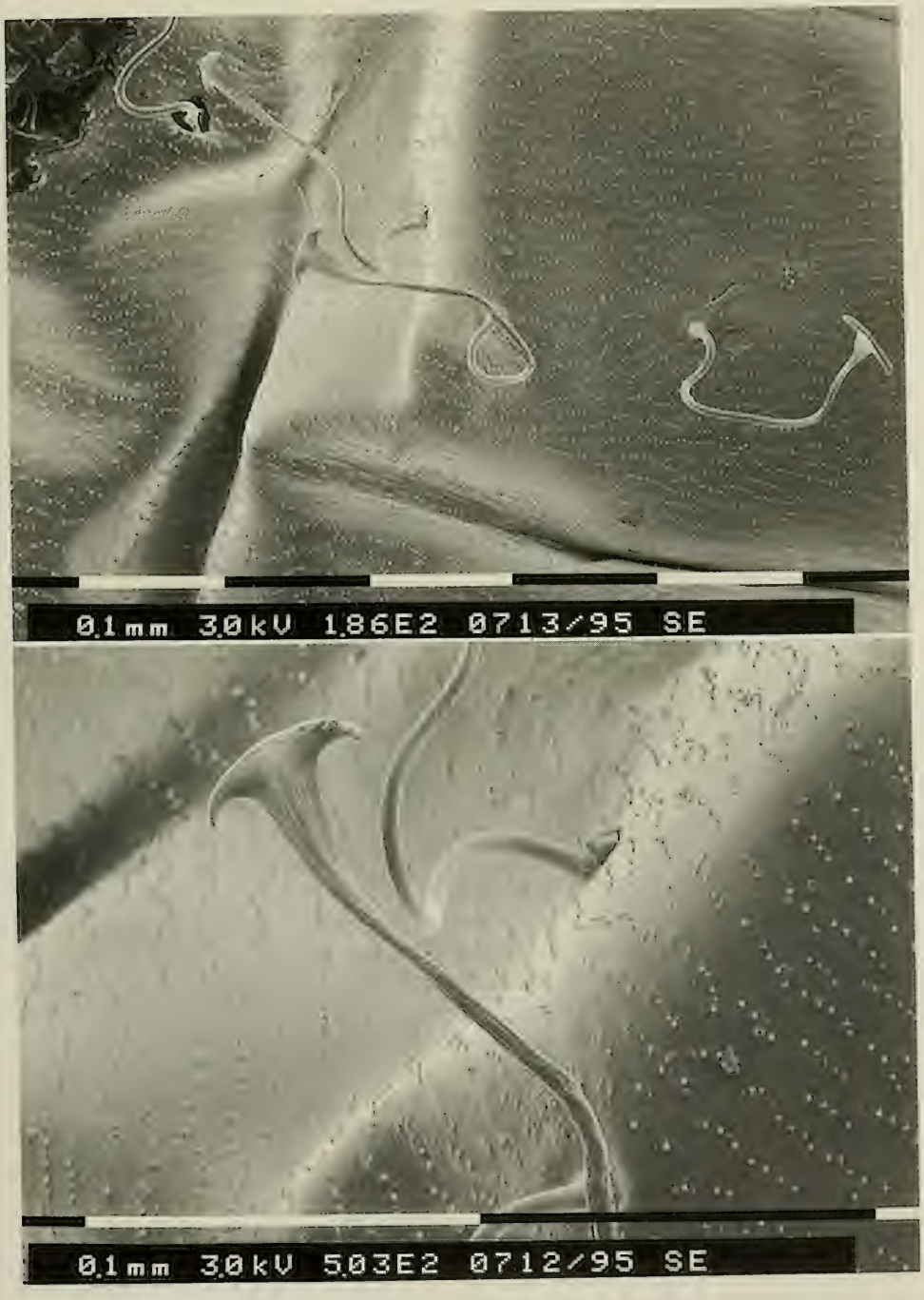


Fig. 20. *Zacryptocerus auricomus* (WHEELER). Larva. Anchor-tipped hairs at two different magnifications. This type of larval hair represents a presumed synapomorphy of the tribe Cephalotini distinguishing it from the morphologically similar and presumably convergent Old World Cataulacini whose larval hairs bear a single terminal hook.

45. Worker. Sting without (0), or with (1) a low dorsal flange.

46. Worker. Sting with indistinct valve chamber even internally (0), or with a reduced valve chamber indistinct in profile but visible internally (1).

47. Worker. Internal apophysis of sting short (0), or long and well sclerotized (1).

48. Worker. Sting base in anterior view flat (0), or more or less arched (1).

49. Worker. Basal ridge of sting absent (0), present but small (1), or large (2).

50. Worker. Articulation of furcula appressed or fused to sting base (0), or free, attached to sting base only at the lateral extremities (1).

51. Male. Cuspis volsellaris present (0), or absent (1). Absence of the cuspis in *Cataulacus* coded after BOLTON (1974).

52. Larva. Dorsal hairs terminating in a single hook (0), or in two (1) (Fig. 20). The distribution of this character has been coded according to WHEELER & WHEELER (1953, 1954 a, 1954 b, 1973 a, 1973 b).

53. Worker (and gyne and male?). Abdominal self-grooming absent (0), or present (1). Presence or absence of this character among the Cephalotini is coded after WHEELER (1984).

Tab. 1. Matrix of the presence (1) and absence (0) of 56 potentially apomorphic characters for the presently recognised genera of Cephalotini and Cataulacini as well as for two outgroup genera. For the character description see text.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Procryptocerus	0	1	0	1	1	0	1	0	0&1	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Cephalotes	0	0	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	0	1	0
Eucryptocerus	0	0	1	0	0	1	1	0	1	1	1	1	0	0	0	1	1	1	1	?	1	1	1	1	1	0	1	0
Zacryptocerus	0	0	1	0&2	0	1	1	0	0&1	1	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0&1
Cataulacus	1	0	0	2	1	0	1	1	0&1	1	0	1	0	1	0	0&1	1	0	1	0	1	0	1	0	1	1	1	0
Myrmecina	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	*	0	0	0	0	1
Pheidole	0	0	0	1	0&1	0	0&1	0	0	0&2	1	0	0	0	2	0&1	0	1	0	1	0	0	*	0&1	0&1	0	1	1

	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Procryptocerus	0	1	1	?	1	1	2	1	1	0	2	0	1	0	0	1	0	0	1	0	2	0	0	1	1	0	1	1
Cephalotes	0	1	1	0&1	0&1	1	2	1&2	2	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	0	0
Eucryptocerus	0	1	1	?	?	1	2	1	2	1	1	1	1	0	0	1	1	0	1	1	1	1	0	?	?	?	?	?
Zacryptocerus	0	1	1	1	1	1	2	1&2	1	1	1&2	1	1	0	0	1&2	1	0	1	0&1	0	0	0	1	1	1	1	0
Cataulacus	1	1	1	0	0	0	0	0	2	1	2	0	0	0	1	0	0	1	0	0	1	0	1	0	?	?	?	?
Myrmecina	0	0	0	0	1	0	1	1	2	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	?	?	?	?
Pheidole	0	0	1	1	0&1	1	1&2	1	0	1	0&1	1	0	0	0	1	0	1	1	1	0&1	0&1	0	1	?	0	0	?

* = character state 0 undemonstrated but very probable.

54. Worker. Adult transport present (1), or absent (0). Presence or absence of this behaviour among the Cephalotini is coded after WHEELER (1984). Absence of transport in *Pheidole* is deduced from the observations of WILSON (1976 a) on *P. dentata* and from those of DROUAL (1983) on *P. desertorum* and *P. hyatti*.

55. Worker (and/or gyne?). Production of trophic eggs present (1), or absent (0). Presence or absence of this behaviour among the Cephalotini is coded after WHEELER (1984). Production of trophic eggs in *Pheidole* is described by PASSERA (1978). In this instance, however, trophic eggs are normally nucleate eggs laid only by virgin queens suggesting a phenomenon completely different from the one reported in *Zacryptocerus* and *Procryptocerus*.

56. Worker. "Abdominal trophallaxis" present (1), or absent (0). Presence or ab-

sence of this behaviour among the Cephalotini is coded after WHEELER (1984). This behaviour, of unknown significance, was described first in *Z. varians* by WILSON (1976 b). In this paper he also proposes a functional explanation for it derived exclusively from the cephalotine morphology. Since the same behaviour has been reported subsequently among some non-cephalotine ants (STUART, 1981), and since the cephalotine *C. atratus* does not exhibit this behaviour (CORN, 1980), this explanation, as already noted by WHEELER (1984), should be abandoned. WILSON (l. c.) considered "abdominal trophallaxis" to be different from the consumption of trophic eggs already known for other ants (e. g. FREELAND, 1958; TOROSSIAN, 1958), the main difference being the fact that the ant licking the proctodeal area of a nestmate goes straight to the abdomen of the "donor" without previous head to head contacts. Because of these uncertainties in interpretation, the "abdominal trophallaxis" has been coded as unknown in all the outgroups.

The presence or absence of these characters among the seven genera included in our analysis is given in Tab. 1. The tranSition between two character states has been assumed to be always unordered for the cladistic analysis.

5.2. Limits and diagnostics of the Cephalotini

The data of Table 1 allow the construction of two equally most parsimonious trees of length 104 (Fig. 21: 1 & 2) (Consistency Index, CI = 0.808, Consistency Index excluding uninformative characters, CI_{inf} = 0.613, Homoplasy Index, HI = 0.413, Homoplasy Index excluding uninformative characters, HI_{inf} = 0.489, Retention Index, RI = 0.556, Rescaled Consistency Index, RC = 0.449). The figure also depicts the tree of strict consensus between the two (Fig. 21: 3) (Tree length 106, CI = 0.792, CI_{inf} = 0.602, HI = 0.425, HI_{inf} = 0.500, RI = 0.511, RC = 0.405).

All these trees share the same topology with respect to the position of the monotypic tribe Cataulacini and of the Cephalotini. The synapomorphies for these clades are listed on the following page.

As one can see, the list of characters synapomorphically shared by the two tribes under the hypothesis of their monophyletic origin is rather impressive. In addition to the eight characters listed above, our data matrix contains 10 additional characters shared symplesiomorphically at the root of this clade thus strengthening the similarity between Cephalotini and Cataulacini. The suspicion might remain, however, that our results may be affected by our failure to extract more information from the data and for not including a still unknown and hypothetically much better outgroup taxon for comparison in the analysis. This appears unlikely if one considers the patristic distances between all taxa included in the analysis (Table 2): the patristic distance between *Procryptocerus* and *Cephalotes*, for example, is of the same order of magnitude as the distance between *Procryptocerus* and *Cataulacus*. It has been already argued that the nearly universal conception of convergence between Cataulacini and Cephalotini was never demonstrated and was probably suggested from their strict geographic vicariance, a situation which is also in perfect agreement with the hypothesis of allopatric speciation of two descents from a unique ancestor.

It must be remembered that in modern times only KUGLER (1978) hypothesised a close relationship between the two tribes: he reached his conclusion after a detailed study of the sting morphology alone. Since in our analysis we indiscriminately used

all characters derived from sting morphology as defined by KUGLER (1978), one may suppose some kind of bias for monophyly in our results. In fact the reverse is true. We re-analysed our data matrix after excluding all the sting characters (characters 25 – 50). The result is an unique most parsimonious tree topologically identical to tree 2 of our Fig. 21. This tree (TL 46) fits the character matrix much better than the trees obtained by including the sting characters: CI = 0.864, CI_{inf} = 0.651, HI = 0.326, HI_{inf} = 0.441, RI = 0.714, RC = 0.621.

We hence consider the monophyletic origin of the Cataulacini and Cephalotini as highly probable.

At the same time, we also regard the individual tribal synapomorphies listed below as largely sufficient to maintain a separate tribal status for both the Cataulacini and the Cephalotini.

Cataulacini alone	Cephalotini alone	Cephalotini + Cataulacini
— Loss of sexual dimorphism	— Male and female proventriculus in form of mushroom	— Female with the oral cavity ventrally deeply incised
— Female eyes above the scrobes	— Female radial cell open	— Female antennae 11-jointed
— Male scape much (>5 times) longer than the first funicular joint	— Worker gonostyli with sensilla basiconica	— Female mandibles thick
— Male antennae 11-jointed	— Worker valve chamber distinct	— Female first gastral tergite expanded
— Worker posterodorsal lobe of the spiracular plate present		— Worker anterior apodeme of the spiracular plate broad
— Worker posterior edge of the quadrate plate emarginate		— Worker posterodorsal edge of the spiracular plate present as a distinct corner
— Worker loss of sensilla trichoidea on the anal plate		— Worker postincision of the oblong plate extending far anteriorly to the dorsal end of fulcral arm
— Worker median tubercle of the triangular plate present		— Female (and male?) ileum dilated and thickened to host micro-organisms (not fully demonstrated)
— Worker reduction of the internal apophysis of the sting		
— Loss of volsellar cuspis		

In the *mare magnum* of unclear supra-generic phylogenetic relationships of the subfamily Myrmicinae the strict relationship between the two tribes Cephalotini and Cataulacini (i. e. their monophyly) appears as one of the few reasonable certainties. The ant literature contains several examples of unjustified suspected convergence among similar taxa. Most of these cases (e. g. the presumed 'diphyly of the Dorylinae') are based on simple intuition drawn from one single, recurring trait: allopatry.

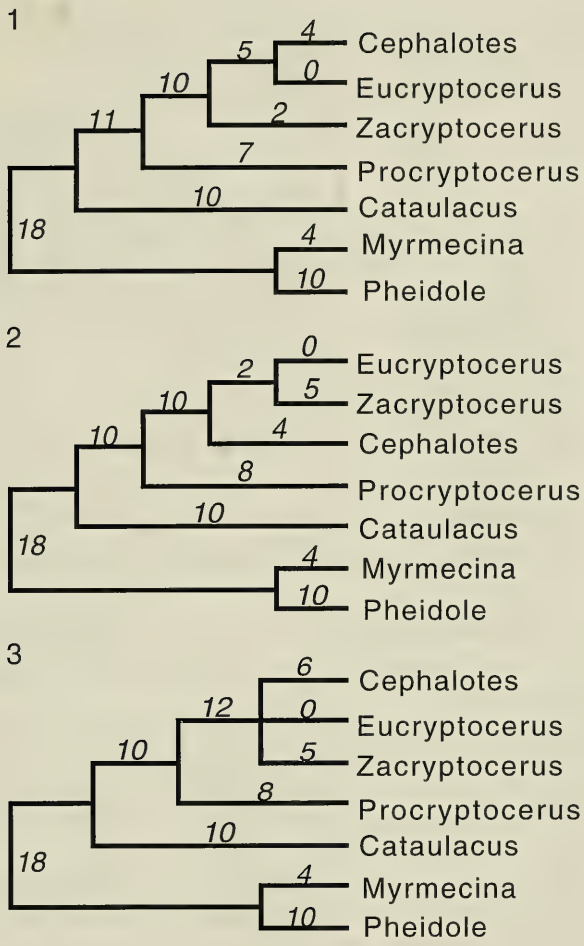


Fig. 21. The two equally most parsimonious phylogenies of the genera considered in the text based on the characters of Table 1 (trees 1 and 2) and their relative strict consensus tree (tree 3). The figures on the branches represent branch lengths.

5.3. The Cephalotini genera

In the following we shall present a discussion of the Cephalotini genera as they are presently understood. We shall show later (Chapter 5.5) that this discussion is largely academic since one of the most relevant taxa involved (*Zacryptocerus*) is very likely to be polyphyletic. This fact removes any significance attached to its current presumed taxonomic status. Indeed we only discuss the status of the "genera" currently considered to constitute the tribe Cephalotini because the presently polyphyletic *Zacryptocerus* could easily be rendered monophyletic by resurrecting the old genus *Hypocryptocerus*. Emendation of *Hypocryptocerus* to a valid genus would inevitably also lead to a rediscussion of the generic status of *Eucryptocerus* and *Zacryptocerus*. We do not consider *Hypocryptocerus* as a valid genus in this paper because we have been totally unable to find plausible genus-level synapomorphies for it.

Tab. 2. Matrix of patristic distances among the taxa discussed in text (character evolution by accelerated transformation, multistate characters excluded from calculations). Above diagonal patristic distances; below diagonal adjusted character distances.

	Procryptocerus	*Cephalotes*	*Eucryptocerus*	*Zacryptocerus*	*Cataulacus*	*Myrmecina*	*Pheidole*
Procryptocerus	*	21	16	19	22	31	24
Cephalotes	19	*	5	8	31	40	33
Eucryptocerus	16	5	*	3	26	35	28
Zacryptocerus	13	8	3	*	29	38	31
Cataulacus	22	24	25	23	*	33	26
Myrmecina	24	29	27	23	24	*	13
Pheidole	18	18	16	16	24	10	*

For the sake of simplicity we reproduce Fig. 21, 1 and Fig. 21, 2 as separate phylograms in Figs. 22 and 23 respectively. From the study of these figures one can draw the following conclusions:

1. There are no known synapomorphies for *Eucryptocerus*. This genus must therefore be considered either as a synonym of *Zacryptocerus* (in the hypothesis of the phylogeny of Fig. 22) or as a synonym of *Cephalotes* (in the hypothesis of the phylogeny of Fig. 23). The latter assumption appears to be intuitively preferable.

2. *Zacryptocerus* can be interpreted in two different ways:

2. 1. According to the phylogeny of Fig. 22 (i. e. including *Eucryptocerus*). In this case it would be characterised by the following two secondary losses in all female castes: migration of the eye from below to behind the antennal scrobe, and antennal scrobes shortened, not reaching the posterior border of the eyes. We regard these characters as potentially significant generic synapomorphies.

2. 2. According to the phylogeny of Fig. 23 (i. e. as the sister genus of *Cephalotes* + *Eucryptocerus*). In this case it would be characterised by only one synapomorphy: the secondary loss of the dorsal notch of the spiracular plate. We do not regard this character as potentially significant at a generic level.

3. *Cephalotes* equally assumes a different phylogenetic significance according to the cladistic reconstruction adopted:

3. 1. In the phylogeny of Fig. 22 it is characterised by the following three synapomorphies: presence of a dorsal tubercle on the triangular plate, presence of a median tubercle on the triangular plate, and secondary loss of the abdominal self-grooming behaviour. We are sceptical of the generic value of all these characters.

3. 2. In the phylogeny of Fig. 23 and including *Eucryptocerus* it is characterised by the following synapomorphies: anterior apodeme of the spiracular plate narrow (an evolutionary inversion) and articulation of the furcula attached to the sting base only laterally. We are only slightly less sceptical of the phylogenetic value of these characters.

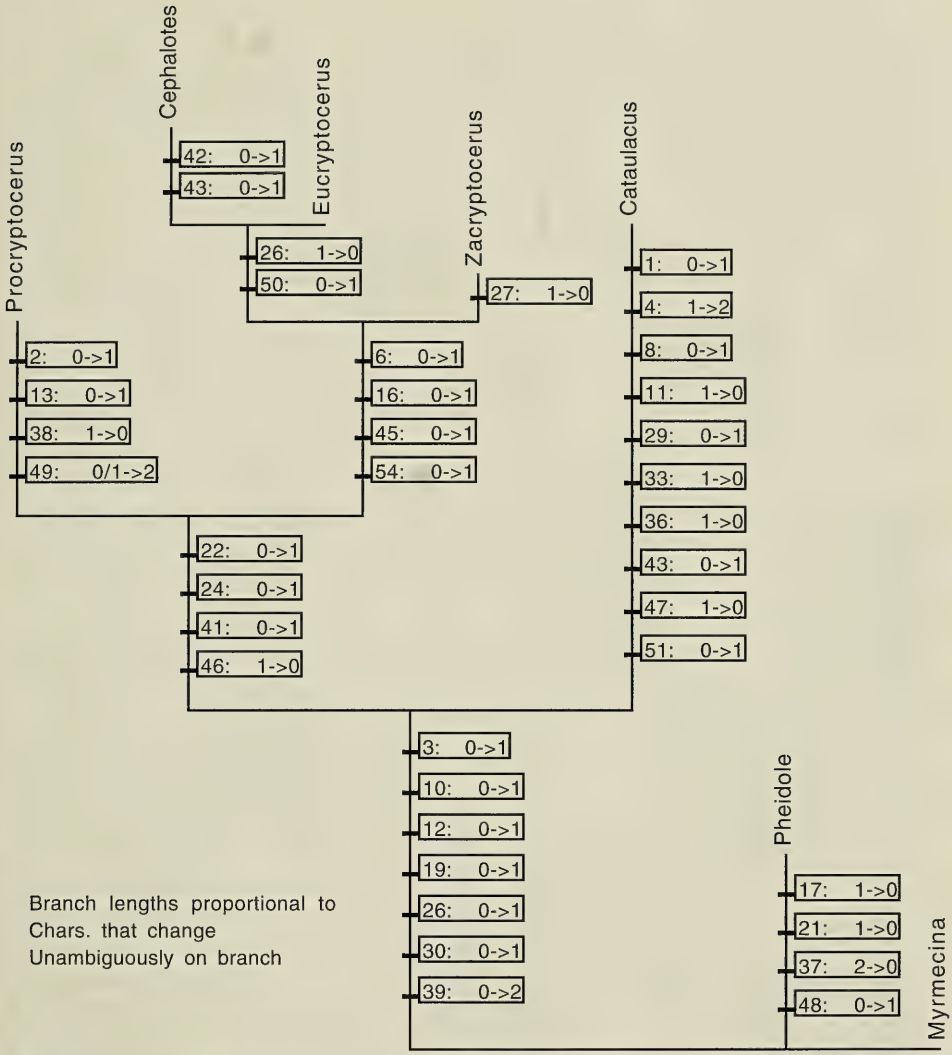


Fig. 22. One of the two possible optimal phylogenies for the genera discussed in the text resulting from a parsimony analysis of the data of Table 1. This is phylogeny 1 of Fig. 21 re-drawn here as a phylogram, i. e. with the length of the different branches proportional to the known number of evolutionary changes. Further explanations in text.

From all these considerations it follows that *Cephalotes*, by showing no unequivocal synapomorphies of potential generic rank, is paraphyletic to *Zacryptocerus* which, by bearing the youngest generic name, should be considered a synonym of the former. This confirms the opinion already intuitively expressed by BROWN (1973) in contrast to KEMPF (1973) and WHEELER (1984).

Since we showed that the apomorphies for *Cephalotes* are too weak to justify generic separation, only the two genera *Procryptocerus* (with 39 described species ranging from Mexico to Argentina) and *Cephalotes* (containing all the other described Cephalotini) can be recognised as valid within the tribe Cephalotini.

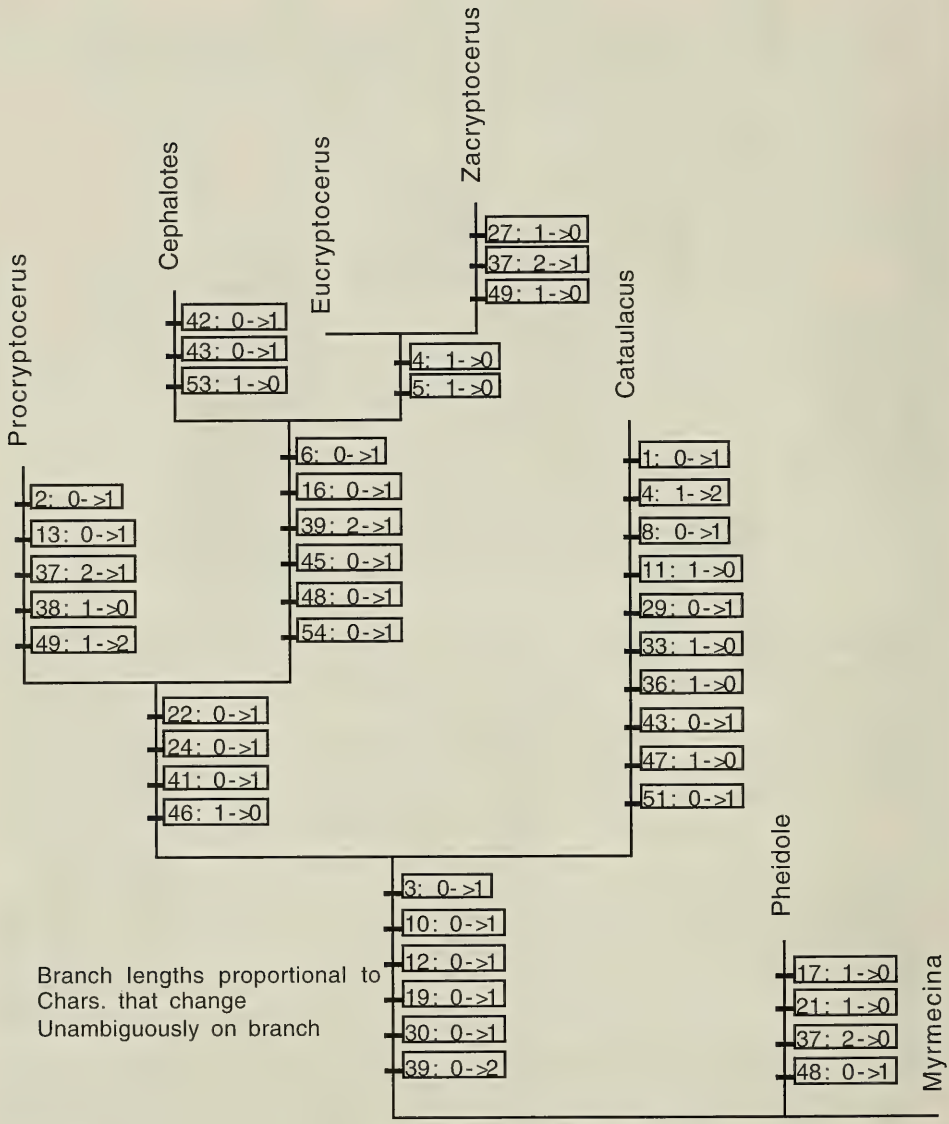


Fig. 23. One of the two possible optimal phylogenies for the genera discussed in the text resulting from a parsimony analysis of the data of Table 1. This is phylogeny 2 of Fig. 21 re-drawn here as a phylogram, i. e. with the length of the different branches proportional to the known number of evolutionary changes. Further explanations in text.

The formal synonymy of the two cephalotine genera we recognise, hence, is as follows:

Cephalotes LATREILLE

Cephalotes LATREILLE, 1802 a: 357. Type species *Formica atrata* LINNAEUS, by monotypy.

Cryptocerus LATREILLE, 1803: 311. Type species *Formica atrata* LINNAEUS, by monotypy. Synonymy by SMITH (1949).

Cryptocerus FABRICIUS, 1804: 418. Type species *Cryptocerus atratus* (LINNAEUS) designated by LATREILLE, 1810: 437. Nec *Cryptocerus umbraculatus* FABRICIUS, designated by EMERY, 1914 b. Synonymy proposed by SMITH (1949).

[*Zacryptocerus* ASHMEAD, 1905: 384. Type species *Cryptocerus multistrigus* SMITH (nomen nudum) by original designation. Unavailable name (Code of Nomenclature, Art. 12).]

Zacryptocerus [ASHMEAD], WHEELER, 1911: 175. Type species *Cryptocerus clypeatus* FABRICIUS. First valid type designation. New synonym. Synonymy resulting from the previous discussion.

Paracryptocerus EMERY, 1915 a: 192 (subgenus of *Cryptocerus*). Type species *Cryptocerus spinosus* MAYR by original designation. New synonym. Synonymy with *Cephalotes* resulting from the one with *Zacryptocerus* proposed by KEMPF (1973).

Cyathocephalus EMERY, 1915 a: 100 (subgenus of *Cryptocerus*). Type species *Cryptocerus pallens* KLUG by original designation. New synonym. Synonymy with *Cephalotes* resulting from the one of its replacement name *Cyathomyrmex* with *Paracryptocerus* (KEMPF, 1972). Junior homonym of *Cyathocephalus* KESSLER, 1868 (Cestoda).

Hypocryptocerus WHEELER, 1920: 53 (subgenus of *Cryptocerus*). Type species *Formica haemorrhoidalis* LATREILLE by original designation. New synonym. Synonymy with *Cephalotes* resulting from the one with *Zacryptocerus* proposed by KEMPF (1973).

Cyathomyrmex CREIGHTON, 1933: 192 (new name for *Cyathocephalus* EMERY). Type species *Cryptocerus pallens* KLUG by original designation. New synonym. Synonymy with *Cephalotes* resulting from the one with *Paracryptocerus* proposed by KEMPF (1972).

Harnedia SMITH, 1949: 20 (subgenus of *Paracryptocerus*). Type species *Cryptocerus umbraculatus* SMITH by original designation. New synonym. Synonymy with *Cephalotes* resulting from the one with *Paracryptocerus* proposed by KEMPF (1972).

Zacryptocerus WHEELER, KEMPF, 1951: 134. Type species *Cryptocerus clypeatus* FABRICIUS designated by WHEELER, 1911:175.

Eucryptocerus KEMPF, 1951: 127. Type species *Cryptocerus oculatus* SPINOLA by original designation. New synonym. Synonymy resulting from the previous discussion.

Exocryptocerus VIERBERGEN & SCHEVEN, 1995: 159. Type species *Exocryptocerus serratus* VIERBERGEN & SCHEVEN by original designation. New synonym. Synonymy resulting from the previous discussion.

Procryptocerus EMERY

Procryptocerus EMERY, 1887: 470 (footnote). Type species *Meranoplus striatus* SMITH, designated by WHEELER, 1911.

These two genera are easily distinguished and the ant literature contains several examples of practical keys useful for separating them. In the following table we give a list of the characters which distinguish unequivocally *Cephalotes* from *Procryptocerus*. The character state appearing as *apomorphic*, in the results of our cladistic analysis is given in italics.

Procryptocerus	*Cephalotes*
— *Male larger than gyne*	— Male smaller than or subequal to gyne
— Female frontal carinae reduced, not covering the genae	— *Female frontal carinae covering most of the genae*
— *Male mandibles strongly convex and apically round*	— Male mandibles reduced and weakly convex, pointed at apex
— Female humeral angles unarmed	— *Female humeral angles with spines or lamellae*
— *Worker, secondary loss of the subterminal tubercle of the oblong plate*	— Worker, subterminal tubercle of the oblong plate present
— Worker, sting without dorsal flange	— *Worker, sting with a dorsal flange*
— Worker, basal ridge of sting absent or reduced	— *Worker, basal ridge of sting large*
— Adult transport behaviour absent	— *Adult transport behaviour present*

We consider it probable that additional synapomorphies will be found for the two genera, particularly when the males of more species become known and studied.

Since all fossil species available to us for the present study belong unequivocally to the genus *Cephalotes* as defined by us in the previous pages, we shall concentrate on this genus only the following discussion.

The 39 known species of *Procryptocerus* show a geographic distribution slightly less extensive than that of the entire Cephalotini.

5.4. Some synapomorphy hypotheses within *Cephalotes*

Most characters useful in identifying *Cephalotes* species, such as the presence, absence, size, and shape of body spines as well as other integumental expansions and microsculpture, colour patterns, etc. are likely to have a clear adaptive, functional significance (see later, Chapter 6.7) and are likely to have been selected for convergently more than once among different (groups of) species. This leads to the astounding situation of a genus whose species exhibit many more diagnostic characters than usual in other ant genera but for which the identification of potential synapomorphic traits is uncertain. In particular, some classic diagnostic characters established in the literature, such as the shape of the hind basitarsi, still proved excellent in separating pairs of species but conflicted with other, probably synapomorphic, characters making them unsuitable for use in phylogenetic reconstructions.

For the sake of simplicity we systematically avoided to include specific autapomorphies in the following list of characters. These will only be described within the individual species treatment. Nonetheless, the secondary loss or the homoplastic gain of some of the characters listed by us as being synapomorphic in this chapter will occasionally prove to be autapomorphic in the inferred phylogenetic reconstruction.

Some characters which could easily have been coded as multistate have been converted into a set of binary characters thus avoiding additive binary coding (see the methods chapter).

Among the many possibilities for tracing plausible synapomorphies within *Cephalotes*, we have retained the characters listed below as being of probable phyloge-

netic significance. The figure in **bold** after each character identification number is the weight attributed to that character for the reasons explained in Chapter 4.2.

1 (**2**). Worker. Frontal carinae over the eyes nearly straight (0) (e. g. Figs. 26 & 171), or with a broad lateral incision (1) (e. g. Figs. 225 & 230). A group of closely related species belonging to KEMPF's "subgroup *wheeleri*", like *rohweri*, *wheeleri*, *insularis*, etc. have only superficially incised frontal carinae and have been coded as "0".

2 (**2**). Worker, soldier and gyne. Frontal carinae laterally without (0), or with a denticle (e. g. Figs. 49 & 55) (1). The species *alfaroi*, where only small workers have denticulate frontal carinae has been coded "0".

3 (**2**). Worker. Frontal carinae not (0), incompletely (1), or completely (2) covering the cheeks in dorsal view. This character, in general, applies well to gynes and (when present) to soldiers as well. Only *alfaroi* and *serraticeps* exhibit state 1 for the workers and 2 for soldiers and gynes. Because of restriction of this character to workers only these species have been coded "1".

4 (**2**). Worker. Frontal carinae coloured like the rest of the head (0), or coloured differently (1).

5 (**1**). Worker. Antennal scrobes, posteriorly, surpassing the posterior border of the eyes (0), or not (1).

6 (**1**). Worker. Vertex without spines at least in the smallest specimens (0), or with (1) a pair of spines even in the smallest specimens.

7 (**2**). Worker. Vertexal angles differently shaped (0), or triangular (e. g. Figs. 108 & 111) (1).

8 (**2**). Worker. Vertexal angles without (0) (e. g. Figs. 71 & 147), or with (1) a narrow, continuous, transparent lamella, (e. g. Figs. 78 & 84), or with (2) (e. g. Figs. 93 & 94) a broad, continuous, transparent lamella. Character state 0 corresponds to the complete absence of vertexal continuous lamellae, or to the presence of spines or membranes or lamellae in which the margin has notch(es).

9 (**2**). Worker (soldier and gyne). Vertexal angles without (0), or with (1) a pair of spines. Presence of this character can be recognised among soldiers and gynes as well but it is much less evident there.

10 (**2**). Worker. Vertexal angles either not round (i. e. bidenticulate, pointed, obtuse, truncate) and, if round, without adjecting crenulation (0), or round and broadly crenulate (1). Character state 1 appears to be one of the few putative synapomorphies discovered so far for the Hispaniolan species of the "*Hypocryptocerus*" species complex.

11 (**2**). Worker. Cephalic index $\leq$ 147.3 (0), or $\geq$ 155.2 (1).

12 (**2**). Worker, soldier and gyne. Postoccipital suture extending over the ventral side of the head (0), or interrupted by a postgenal bridge (1).

13 (**2**). Worker, (soldier and gyne). Eye position: below (0), or behind or above (1) the antennal scrobes. Character state 0 is one of the classical putative generic characters distinguishing the "genera" *Cephalotes* s. str. and *Procryptocerus* from all other Cephalotini. This character appears to be rather constant; the main discrepancy can be found among the species *clypeatus*, *ustus* and *membranaceus* where the workers have the eyes above and the soldiers and gynes behind the antennal scrobes.

14 (**2**). Worker. Eye size: maximum diameter smaller (0), or greater (1) than 1/3 of median head length.

15 (1). Worker. Ventral and lateral faces of the head longitudinally sculptured (0), with marked zigzag striation (1), or differently sculptured (2). Presence of only lateral longitudinal rugosity is coded as 2.

16 (2). Worker. Ventral face of the head differently sculptured (0), or with superficial reticulation only (1).

17 (2). (Worker), soldier and gyne. Mandibles without (0) (e. g. Figs. 26 & 63), or with a lateral swelling, carina, or denticle (1) (e. g. Figs. 60, 137, 156). This character, always clear among soldiers and gynes, in a few species like *cordiventris* and *manni*, may be difficult to appreciate among workers. For this reason, *solidus*, known on five workers only, has been conservatively coded as "?". In fact we have been unable to detect with certainty the presence of a carina among these five specimens but we don't regard the evidence available as sufficient to guarantee that soldiers and gynes may not present a carina, once they will be discovered. We describe this character as non caste-dependant and consider also workers in its description for the two following reasons: 1) the difficulty of detection of the carina among workers is more an exception than the rule, and, 2) to be able to include in our analysis other species, known only on workers, and for which the presence of this character is clear. As a matter of fact, we experimentally re-made our analysis twice after coding *solidus* respectively as "0" and "1" for this character and we obtained no topological changes in the resulting trees.

18 (2). Worker and gyne. Maxillary palps in relaxed position extending posteriorly over the hypostomal bridge (0), or not reaching it (1).

19 (2). Worker, soldier and gyne. Antennal club of three (0), or two (1) joints. In some species (e. g. *bimaculatus*) this character is more difficult to appreciate for soldiers and gynes than for workers. Workers of *guayaki* and *quadratus* have a three-jointed club but careful examination from all sides is necessary to ascertain this condition.

20 (2). Worker. Mesosoma variously but never regularly longitudinally striate (0), or regularly longitudinally striate, the striae parallel and never anastomosing (1).

21 (2). Worker. Scapular angles in dorsal view visible (0), or hidden by parts or expansions of the pronotum (1).

22 (2). Worker. Pronotum, in profile, flat to slightly convex (0), or strongly convex (1).

23 (2). Worker and soldier. Pronotum without (0), or with a pair of dorsal spines (1). State 1 of this character should be synapomorphic for the former genera *Cephalotes* and *Eucryptocerus*. The small workers of *atratus*, *serraticeps* and *alfaroi*, however, are without middle pronotal spines.

24 (2). Worker. Pronotum without (0), or with only one lateral spine covered by and fused with a semi-transparent lamella or crest (1).

25 (2). Worker. Pronotum, laterally, with a differently shaped and differently pigmented lamella, or spinose, or with a pigmented crest (0), or with a depigmented, semitransparent, membranaceous crest along the whole sides (1).

26 (2). Worker. Pronotal crest long, i. e. bordering the whole pronotal sides (Char. 25, state 1), caudally, followed by a mesonotal tooth narrowly separate from the crest itself (e. g. Figs. 192 & 197) (0), or followed by a mesonotal tooth broadly separate from the crest (e. g. Figs. 167 & 169) (1). Species without long, depigmented crest coded as "?".

27 (2). Worker. Pronotal lamellae never rectangular, or, if rectangular, broader than the maximum length of the petiole and, if narrower, never followed by a tooth

(e. g. Figs. 134, 139 & 147) (0) or with the following morphological arrangement: rectangular, narrower than the petiolar length and followed by a tooth (e. g. Figs. 155 & 158) (1). Species without lamellae coded as "?".

28 (2). Worker. Pronotum without (e. g. Figs. 181 & 264) (0), or with (1) a lateral spine followed or not by minute denticles (e. g. Figs. 53 & 62).

29 (2). Worker. Pronotum, laterally, without (e. g. Figs. 72 & 84) (0), or with two distinct spines (e. g. Figs. 85 & 90) (1).

30 (2). Worker. Pronotal lamella broad, continuous or at most obtuse anteriorly (e. g. Figs. 99 & 102) (0), or variably denticulate on its whole width (e. g. Figs. 78 & 275) (1). Species without lamellae or with rectangular lamellae followed by a tooth coded as "?".

31 (2). Worker. Second pair of pronotal teeth absent or reduced (0), or thick, broad, triangular and upturned (1).

32 (2). Worker. Mesonotum with no or with one pair of projecting teeth, if two pairs of teeth present, the second pair very small (e. g. Figs. 44, 169 & 194) (0), or with two pairs of well developed teeth, subequal in length (e. g. Figs. 198 & 201) (1).

33 (2). Worker. Propodeal depigmented (membranaceous) crest absent (0), present, not broadening medially and present along the whole sides (1), or present and convex, broadening medially and continuing along the whole propodeal sides (2).

34 (2). Worker. Propodeal depigmented lamella or tooth absent (e. g. Figs. 256 & 259) (0), or present and beginning at some distance after the basal face (e. g. Figs. 126 & 132) (1).

35 (2). Worker. Lateral propodeal lamella or tooth posteriorly straight (e.g. Figs. 126 & 130) (0), or concave (e. g. Figs. 132 & 134) (1). Species without lamella coded "?".

36 (2). Worker. Propodeal pigmented (membranaceous) crest absent or at most reduced to a narrow margin (e. g. Figs. 147 & 209) (0), or present with at least two denticles on the sides (e. g. Figs. 225 & 230) (1), or present and convex, broadening medially (e. g. Figs. 222 & 235) (2).

37 (2). Worker. Propodeum, laterally regularly neither angulate nor with 1-2 small denticles (0), or with a short lateral angle or with 1-2 small denticles (1).

38 (2). Worker. Propodeum, laterally, without (e. g. Figs. 27 & 84) (0), or with (e. g. Figs. 108 & 111) (1) a denticle followed by two spines.

39 (2). Worker. Propodeum, laterally, without (0), or with (1) three well defined denticles.

40 (2). Worker. Propodeum, laterally, without (0), or with (1) four well defined denticles.

41 (2). Worker. Propodeum, laterally, without (0), or with (1) five well defined denticles.

42 (2). Worker. Propodeum, laterally, without (0), or with (1) six well defined denticles.

43 (2). Worker. Propodeum, laterally, without (0), or with a well developed spine followed by a tooth (1).

44 (2). Worker. Propodeum without (0), or with a pair of spines fused with the propodeal lamella (1).

45 (2). Worker. Propodeum, posteriorly, making with the anterior face of the petiole in relaxed position an angle $\leq 100°$ (0), or $>110°$ (1).

46 (2). Worker. Basal and declivous faces of the propodeum not separate (0), or clearly separate by a spine shorter than 2/3 of the length of the basal face (1), or separate by a spine long at least 2/3 of the length of the basal face (2).

47 (2). Worker. Petiole and postpetiole laterally unarmed (0), or armed with spines or teeth or denticles (1), or with broad, membranaceous, depigmented expansions (2).

48 (2). Worker. Petiolar and postpetiolar spines differently shaped but never thin and needle-shaped (0), or thin and needle-shaped (1).

49 (2). Worker. Petiolar dorsum without (0), or with (1) a median longitudinal carina.

50 (2). Worker. Petiole anteriorly angulate, i. e. with distinct anterior and dorsal faces (e. g. Figs. 35 & 108) (0), or anteriorly round, i. e. with indistinct anterior and dorsal faces and the anterior face separate from the lateral ones by an angle (e. g. Figs. 132 & 153) (1), or anteriorly round and the anterior face not separate from the lateral ones and continuing into them with a curve (e. g. Figs. 139 & 147) (2).

51 (2). Worker. Petiole laterally unarmed (0), or armed with a pair of lateral spines or expansions long at most 1/3 of the maximum petiolar length (1), or with lateral spines longer than 1/3 and shorter than 1.3 times the maximum petiolar length (2), or equal to or longer than 1.5 the maximum petiolar length (3). Species with lateral membranaceous expansions coded as "?".

52 (2). Worker and soldier. Postpetiolar expansions either membranaceous or lamellaceous, never broad and pointed posteriorly (e. g. Figs. 90 & 112) (0), or with broad, solid, lateral expansion pointed posteriorly (e. g. Figs. 289 & 291) (1).

53 (2). Worker. Postpetiole with pointed or membranaceous, lateral expansions (0), or with solid, broad lateral expansion with crenulate border (1), or with solid, broad lateral expansion with simply round border (2).

54 (2). Worker. Spiniform, lamellaceous expansions of the postpetiole shorter than its node (0), or longer than its node (1).

55 (2). Worker. Postpetiolar node convex, or, if flat, without a pair of erect, clubbed hairs on the posterior border (0), or flat and with a pair of erect, clubbed hairs on the posterior border (1).

56 (2). Worker, soldier and gyne. Fore coxae round (0), or protruding or angulate or dentate anteriorly (1). For some species of the *complanatus*-group this character is better visible in soldiers and gynes.

57 (2). Worker. Fore femora incrassate but without deep ventral groove to receive the tibiae (0), or incrassate and with a deep ventral groove to receive the tibiae (1), or slender (2).

58 (2). Worker. Fore femora rounded (0), or with a broad ventral crest (1).

59 (2). Worker, soldier and gyne. Hind femora externally curved (0), or clearly angulate, or denticulate, or crested on the outer face (1). For some species this character is better visible in workers.

60 (2). Worker. Extensor face of the tibiae of the three pairs of legs without (0), or with (1) longitudinal, irregular rugulation.

61 (1). Worker. HBaI $\leq$ 53.3 (0), or $\geq$ 57.0 (1).

62 (1). Worker. Gaster without expansions or with solid lobes or with reduced lamellar or crested expansions (0), or lamellar expansion of the gaster well developed reaching, anteriorly, the posterior face of the postpetiole and surpassing the stigma posteriorly (1).

63 (2). Worker. Anterior gastral expansions differently shaped but never bent ventrally (0), or bent ventrally (1). Species without anterior gastral expansions have been coded as "?".

64 (2). Worker. Anterior gastral expansions differently shaped but never bent dorsally neither touching the postpetiolar lateral expansions (0), or with the anterior margin membranaceous, bent dorsally and, as a result, slightly concave, overlapping the postpetiolar lateral expansions (1). Species without anterior gastral expansions have been coded as "?".

65 (2). Worker. Lobe of the anterior gastral expansions membranaceous or absent (e. g. Figs. 192 & 247) (0), or continuing without interruption into the rest of the gaster (e. g. Figs. 291 & 299) (1), or narrowing posteriorly in a "neck" interrupting the lateral profile of the gaster (e. g. Figs. 309 & 311) (2). Species without anterior gastral expansions have been coded as "?".

66 (2). Worker. First gastral tergite with the lateral and posterior border con colour with the rest of the tergite (0), or transparent-yellowish (1).

67 (2). Worker. First gastral tergite, smooth, rugulose, or reticulate (0), or mostly covered by longitudinal striae (1).

68 (2). Worker. Striation of the first gastral tergite absent or differently extended but never limited to the anterior fourth (0), or present on the anterior fourth only (1). Species with first gastral tergite covered by longitudinal rugosities coded as "?".

69 (1). Worker. First gastral sternite without longitudinal striation (0), with longitudinal striation on the anterior third and on the sides (1).

70 (2). Worker. Gaster concolour with the rest of the body (0), or differently coloured than the rest of the body (1).

71 (1). Worker. Gaster without (0), or with two anterolateral yellow or reddish spots or strips (1).

72 (2). Worker. Vertex deeply and irregularly foveolate, without (0), or with curved, subclavate hairs (1).

73 (2). Worker. Vertex without broad clavate hairs (0), or with broad clavate hairs (1).

74 (1). Worker. Gaster without (0), or with (1) two anterolateral tufts of dense, silvery hairs.

75 (2). Worker. Truncate hairs absent (0), or present (1).

76 (2). Worker. Long and flexuous hairs absent (0), or present (1).

77 (2). Worker. Thick, long, appressed golden hairs on the gaster absent (0), or present (1).

78 (2). Soldier caste absent (0), or present (1).

N o t e : all species without soldier caste have been coded as "?" for the following characters: 79, 82, 84, 86, 87, 89 – 98, 100 – 109.

79 (2). Soldier. Frontal carinae not reaching (0), or reaching (1) the vertexal angles backwards.

80 (1). Soldier and gyne. Antennal scrobes, posteriorly, surpassing the posterior border of the eyes (0), or not (1). This character, equivalent to char. 5, codes differently in workers as in soldiers and gynes.

81 (2). Soldier and gyne. Vertexal angles without (0), or with (1) a broad, transparent, not crenulate lamella.

82 (1). Soldier. Vertex unarmed (0), or bispinose (1).

83 (2). Soldier and/or gyne. Vertex straight (0), or medially depressed (1). This character, sometimes, may be difficult to appreciate since the median depression can be very reduced or present in one caste only. In some species the depression is better visible among gynes than among soldiers. Species like *alfaroi*, *bohlsi*, *chacmul*, *conspersus*, *foliaceus*, *goniodontus*, *manni*, *olmecus*, *palta*, *palustris*, *quadratus*, *simillimus*, *toltecus*, *ustus*, and *wheeleri* known only on soldiers without vertexal depression and for which the gyne is still unknown have been coded "?". Species like *inca* and *ecuadorialis* for which only the gynes and not the soldiers are known are also coded "?". Species in which only one caste is known but in which the known caste shows the median depression are coded "1".

84 (1). Soldier. Cephalic disc absent (0), incomplete (i. e. poorly differentiate, particularly on the sides) (1), or complete (2). This character is better visible in maximum size soldiers.

85 (2). Soldier and gyne. Cephalic disc not covering (0), or covering (1) the mandibles in dorsal view. Species without cephalic disc coded as "?".

86 (2). Soldier. Floor of the cephalic disc flat and/or concave (0), or convex (1). *C. angustus* and *jheringi* have been coded as polymorphic for this character since there are specimens with flat disc and specimens with convex disc. Species without cephalic disc coded as "?".

87 (2). Soldier. Floor of the cephalic disc flat and/or concave (= character 86 state 0) (0), or deeply perpendicular anteriorly (e. g. Fig. 268) (1). Species without cephalic disc or with convex disc (character 86 state 1) coded as "?".

88 (2). Soldier and gyne. Sides of the cephalic disc without (0), or with a longitudinal, carina with a denticle protruding ventrally into the antennal scrobes (1). This character should be observed among large soldiers and gynes. Species with incomplete carina in the soldier and complete carina in the gyne have been coded as "0". Species without cephalic disc coded as "?".

89 (2). Soldier. Sides of the frontal carinae without (0), or with hairs (1).

90 (2). Soldier. Cephalic disc covering the mandibles (character 85, state 1) without a row of long, appressed hairs on the internal border (0), or with a row of long appressed hairs on the internal border (1). Species without disc or with disc not covering the mandibles have been coded as "?".

91 (2). Soldier. Antennal scrobes terminating posteriorly in front of the eyes (0), or below the eyes (1).

92 (2). Soldier. Floor of the cephalic disc concave or flat (character 86, state 0) and with foveae separate by distinct interspaces (0), or with contiguous foveae (1). *C. angustus* and *jheringi* which possess soldiers with flat or convex disc (coded as polymorphic for character 86) and which have foveae interspaced (*angustus*) or contiguous (*jheringi*) have been coded respectively 0 and 1. This character applies better to large soldiers than to small ones (e. g. *porrasi*). Species without disc or with convex disc have been coded as "?".

93 (2). Soldier. Floor of the cephalic disc concave or flat (character 86, state 0) with the hairs not surpassing the foveal border (0), or with hairs largely surpassing the foveal border (1). Species without disc or with convex disc coded as "?".

94 (2). Soldier. Cephalic disc concave and with contiguous foveae (character 90, state 1), the foveae superficial and bearing appressed hairs (0), or deep, bearing suberect hairs not surpassing the foveal border (1). Species without disc or with convex disc have been coded as "?".

95 (2). Soldier. Cephalic disc convex (character 86, state 1) and with foveae separated by distinct interspaces (0), or with contiguous foveae (1).

96 (2). Soldier. Cephalic disc convex (character 86, state 1) and with foveae bearing only one type of hairs (0), or bearing two types of hairs (1). *C. angustus* and *jheringi* which possess flat and convex disc with only one type of hairs have been coded as (0). Species with flat or concave disc or without disc coded as "?".

97 (2). Soldier. Cephalic disc convex (character 86, state 1) with foveae bearing decumbent hairs (0), or with suberect hairs (1). Species with flat or concave disc or without disc coded as "?".

98 (2). Soldier. Cephalic disc convex (character 86, state 1) with the frontal carinae bearing clavate hairs (0), or with the frontal carinae with pointed hairs (1). Species with flat or concave disc or without disc coded as "?".

99 (2). Soldier and gyne. Head concolour (0), or bicolour (1).

100 (1). Soldier. Ventral face of the head without longitudinal striae (0), or with longitudinal striae (1). This character applies better to large soldiers.

101 (2). Soldier. Pronotum concolour (0), or bicolour (1).

102 (2). Soldier and gyne. Basal face of the propodeum without (0), or with one-two, lateral plate-like projections followed by a spine (1).

103 (2). Soldier. Sides of the basal face of the propodeum without (0), or with (1) two-three pairs of irregular teeth.

104 (2). Soldier. Propodeal lateral teeth absent or of different shape but never curved upwards(0), or strongly curved upwards (1). This character for most of the species applies better to large soldiers. *C. patei* has the teeth slightly directed upwards and has been coded as "1".

105 (2). Soldier. Hind femora smooth (0), or with a carina (1), or with a marked crest (2).

106 (1). Soldier. HBaI $\leq$48.5 (0), or $\geq$ 51.2 (1).

107 (1). Soldier. Gaster flattened or, at most, gently convex, without or with a short crest or lamella (0), or globose, and with a broad anterolateral lamella (1).

108 (2). Soldier. First gastral tergite shorter, or, at most as long as the mesosoma (0), or at least 1.4 longer than the mesosoma (1).

109 (1). Soldier. Gaster without (0), or with (1) two anterolateral tufts of dense, silvery hairs. Note: this character is the same as character 74 but its distribution among workers and soldiers is different.

110 (2). Gyne. HL $\leq$3.0 mm (0), or HL $\geq$3.3 mm (1).

111 (1). Gyne. Cephalic disc absent (0), incomplete (1), or wholly developed (2).

112 (2). Gyne. Cephalic disc convex and without strongly crenulate border (0), or convex and with strongly crenulate border (1). Species without disc or with flat or concave disc have been coded as "?".

113 (2). Gyne. Cephalic disc differently shaped but never concave anteriorly and flat in the posterior fourth (0), or anteriorly concave up to the level of the eyes and flat posteriorly (1).

114 (2). Gyne. Median vertexal depression (character 81, state 1) not reaching the border of the disc (0), or reaching it (1). Species without disc and without median depression on the vertex have been coded as "?".

115 (2). Gyne. Propodeal spines absent or directed backwards (0), or diverging externally (1).

116 (1). Gyne. First gastral sternite with the sides without longitudinal striation at least on part of their surface (0), or with longitudinal striation covering the whole sides of the sternite (1).

117 (1). Gyne. First gastral tergite without coloured spots (0), or with a pair of proximal coloured spots (1), or with two pairs (proximal and distal) coloured spots (2). This character can be properly appreciated only in mature, wholly pigmented, gynes. The available gynes of *supercilii* (one) and of *bruchi* (two) have only the two posterior pairs of spots. In general, when only two gastral spots are present, these are the anterior pair. Other species for which we had more abundant material may present the two posterior spots only as a variation of the "normal" four spots condition. But, since the coloration of the gynes and soldiers is often similar or parallel, and, since the soldiers of both critical species, *supercilii* and *bruchi*, are uniformly dark, these two species were coded as "?".

118 (2). Gyne. First gastral tergite without (0), or with only one median pair of brown spots (1).

119 (2). Male. Subequal in size to the gyne (0), or smaller (1).

120 (2). Male. Mandibles laterally convex (0), or straight (1).

121 (2). Male. Antennal scape at least three times as long as the first funicular joint (0), or never more than twice the first funicular joint (1).

122 (2). Male. Propodeum completely unarmed (0), or armed at least with a pair of obtuse angles or denticles (1).

123 (2). Male. PPeI (Petiolar index) $\leq$ 206 (0), or PPeI $\geq$ 219 (1). Four species with intermediate values (*marginatus*, *varians*, *pellans* and *pilosus*) have been coded as polymorphic for this character.

124 (2). Male. Stipes (THOMSON, 1871; = gonostylus, MICHENER, 1956) short, surpassing the median parameres (= laminae volsellares of SNODGRASS, 1941) for less than half of its length (e. g. Figs. 185 & 338) (0), or very long, surpassing the median parameres of more than half of its length (e. g. Figs. 89 & 296) (1).

125 (2). Male. Digitus volsellaris "normally" angulate dorsally (e. g. Figs. 118 & 163) (0), or simply curved dorsally, without distinguishable angle (Figs. 30 & 34) (1).

126 (2). Male. Internal border of the aedeagus ventrally straight, at most slightly concave (e. g. Figs. 51 & 118) (0), or clearly concave (e. g. Figs. 39 & 166) (1), or with a deep concavity (e. g. Figs. 157 & 163) (2).

127 (2). Male. Internal border of the aedeagus dorsally straight, at most slightly concave (e. g. Figs. 136 & 304) (0), or narrowly concave (Fig. 280) (1). The male of *texanus*, unknown to us, has been tentatively coded as "1" according to a drawing of KRAFCHICK (1959).

128 (2). Male. Internal border of the aedeagus distally undifferentiated (e. g. Figs. 125 & 333) (0), or followed by a tumuliform projection (Figs. 67 & 69) (1).

129 (2). Male. Internal border of the aedeagus interrupted (e. g. Figs. 34 & 326) (0), or reaching the apical tooth (e. g. Figs. 57 & 61) (1).

130 (2). Male. Ventral border of the aedeagus with a row of short teeth (e. g. Figs. 152 & 221) (0), or with a row of long teeth not hidden by the distal projection (e. g. Figs. 89 & 97) (1), or with a row of long teeth partially hidden by the distal projection (Figs. 67 & 69) (2).

131 (2). Male. Distal projection of the aedeagus without a group of denticles (e. g. Figs. 125 & 136) (0), or with a group of denticles (e. g. Figs. 82 & 97) (1).

Tab. 3.1. Matrix of the character states among the *Cephalotes* species and four outgroups.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
adolphi	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	1	1	1	0	0	1	0	0	0	0	?
alfaroi	0	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	1	1	0	0	1	0	01	0	0	?
angustus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
argentiventris	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	?
atratus	0	0	2	1	0	0	0	0	1	0	0	0	0	0	2	0	1	1	0	0	1	0	01	0	0	?
auriger	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	0	?
auricomus	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	?
basalis	0	0	2	0	1	0	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?
betoi	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
biguttatus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
bimaculatus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
bivestitus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
bohlsi	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
borgmeieri	0	0	2	01	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
bruchi	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
chacmul	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	1	0	0	0	0	?
christopherseni	0	0	2	1	1	0	0	2	0	0	0	1	1	0	2	1	0	1	0	0	1	0	0	0	0	?
clypeatus	0	0	2	1	1	0	1	0	0	0	1	1	1	0	2	0	1	1	0	0	0	0	0	1	0	?
coffeae	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
columbicus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	0	1	0	0	1	0	0	0	0	?
complanatus	0	0	2	0	1	0	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?
conspersus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
cordatus	0	0	2	1	1	0	0	01	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
cordiae	0	0	2	0	1	0	0	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?
cordiventris	0	0	2	0	1	0	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?
crenaticeps	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
cristatus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
curvistriatus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	?
decolor	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
decoloratus	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
dentidorsum	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	1	1	1	0	0	1	0	0	0	0	?
depressus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
duckei	0	0	2	1	1	0	0	1	0	0	0	1	1	0	2	1	1	1	0	0	1	0	0	0	0	?
ecuadorialis	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
eduarduli	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
emeryi	0	0	2	0	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
femoralis	0	0	2	1	1	0	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?
fiebrigi	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	1	0	0	0	?
flavigaster	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	?
foliaceus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	1
fossithorax	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
frigidus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
goeldii	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
goniodontus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
grandinosus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
guayaki	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	1	0	0	0	?
hamulus	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	?
hirsutus	0	0	2	1	1	0	0	0	0	0	0	0	1	0	2	0	1	1	1	0	0	0	0	0	0	?
inaequalis	0	0	2	1	1	0	0	2	0	0	0	1	1	0	2	1	0	1	0	0	1	0	0	0	0	?
inca	0	0	2	0	1	0	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?
incertus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	1
insularis	0	0	2	1	1	0	0	0	0	0	0	0	1	0	2	0	1	1	1	0	0	0	0	0	0	?
jamaicensis	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
jheringi	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
klugi	?	0	?	?	?	?	?	?	?	?	?	1	1	?	?	?	1	1	1	?	?	?	?	?	?	?
kukulcan	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
laminatus	0	0	2	1	1	0	0	2	0	0	0	1	1	0	2	1	0	1	0	0	1	0	0	0	0	?
lanuginosus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
lenca	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	?
liepini	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
liogaster	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
maculatus	0	0	2	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0
manni	0	0	2	1	1	0	0	0	0	0	0	1	1	1	2	1	1	1	0	0	0	0	0	0	0	?
marginatus	0	0	2	1	0	0	0	0	1	0	0	0	0	0	2	0	1	1	0	0	1	0	1	0	0	?
membranaceus	0	0	2	1	1	0	1	0	0	0	1	1	1	0	2	0	1	1	0	0	0	0	0	1	0	?
minutus	0	0	2	1	1	0	0	1	0	0	0	1	1	1	2	1	0	1	0	0	1	0	0	0	0	?
mompox	0	0	2	0	1	0	1	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?

Tab. 3.2. Matrix of the character states among the *Cephalotes* species and four outgroups.

	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
adolphi	0	0	0	1	1	0	0	0	?	0	0	0	?	1	0	0	0	0	0	0	1	0	0	0	2	0
alfaroi	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
angustus	0	0	0	1	0	0	0	0	?	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	2	0
argentiventris	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
atratus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0
auriger	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0
auricomus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
basalis	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	3	0
betoi	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	2	0
biguttatus	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0
bimaculatus	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
bivestitus	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1
bohlsi	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
borgmeieri	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	2	3	0
bruchi	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1
chacmul	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0
christopherseni	?	0	1	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	12	0
clypeatus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	01	0	02	1	0	0	0	2	0
coffeae	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0
columbicus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	01	0
complanatus	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	3	0
conspersus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	2	0
cordatus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	2	2	0
cordiae	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	3	0
cordiventris	0	0	0	1	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	23	0
crenaticeps	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
cristatus	1	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	2	0
curvistriatus	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0
decolor	0	0	0	?	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
decoloratus	0	0	0	?	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
dentidorsum	0	0	0	1	1	0	0	0	?	0	0	0	?	1	0	0	0	0	0	0	1	0	0	0	2	0
depressus	1	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	2	0
duckei	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	2	0
ecuadorialis	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
eduarduli	1	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	2	0
emeryi	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
femoralis	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	3	0
fiebrigi	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
flavigaster	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
foliaceus	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
fossithorax	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
frigidus	0	0	0	1	0	0	0	0	?	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	2	0
goeldii	0	0	0	1	0	0	0	0	?	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	0
goniodontus	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0
grandinosus	0	0	0	?	0	1	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
guayaki	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
hamulus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
hirsutus	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0
inaequalis	?	0	1	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	2	0
inca	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	3	0
incertus	0	0	0	?	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
insularis	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0
jamaicensis	0	0	0	?	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
jheringi	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	12	1
klugi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
kukulcan	0	0	0	?	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
laminatus	?	0	1	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	2	0
lanuginosus	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
lenca	0	0	0	1	0	0	0	0	?	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	2	0
liepini	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
liogaster	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
maculatus	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
manni	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0
marginatus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
membranaceus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	2	0
minutus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	2	0
mompox	0	0	0	1	0	0	0	0	?	0	0	1	0	0	0	0	0	0	0	1	1	0	1	0	23	0

Tab. 3.3. Matrix of the character states among the *Cephalotes* species and four outgroups.

	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
adolphi	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	?
alfaroi	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
angustus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
argentiventris	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?
atratus	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
auriger	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	?
auricomus	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
basalis	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1
betoi	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
biguttatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
bimaculatus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1
bivestitus	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
bohlsi	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
borgmeieri	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
bruchi	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
chacmul	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1
christopherseni	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
clypeatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
coffeae	0	0	1	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1
columbicus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
complanatus	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
conspersus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
cordatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
cordiae	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
cordiventris	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
crenaticeps	0	0	0	1	2	0	0	0	0	0	?	?	?	0	0	0	1	0	1	0	0	0	1	0	0	1
cristatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
curvistriatus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1
decolor	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
decoloratus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
dentidorsum	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	?
depressus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
duckei	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
ecuadorialis	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	?
eduarduli	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
emeryi	0	0	0	1	2	0	0	0	0	0	?	?	?	0	0	0	1	0	0	0	0	0	1	0	0	?
femoralis	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
fiebrigi	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
flavigaster	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	?
foliaceus	0	0	0	1	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
fossitborax	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
frigidus	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
goeldii	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
goniodontus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
grandinosus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
guayaki	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
hamulus	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	?
hirsutus	0	0	0	1	2	0	0	0	0	0	?	?	?	1	1	?	1	0	0	0	0	0	0	0	1	?
inaequalis	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
inca	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	?
incertus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
insularis	0	0	0	1	2	0	0	0	0	0	?	?	?	1	1	?	1	0	1	0	0	0	0	0	0	1
jamaicensis	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
jheringi	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
klugi	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
kukulcan	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
laminatus	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
lanuginosus	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	1
lenca	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	?
liepini	0	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	1
liogaster	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	1
maculatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1
manni	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
marginatus	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
membranaceus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
minutus	0	0	0	1	2	0	01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
mompox	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?

Tab. 3.4. Matrix of the character states among the *Cephalotes* species and four outgroups.

	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104
adolphi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
alfaroi	1	1	0	1	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	0
angustus	1	1	0	0	0	2	0	01	0	1	1	?	0	0	0	0	0	0	0	0	1	0	1	0	0	1
argentiventris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
atratus	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
auriger	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
auricomus	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
basalis	1	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
betoi	1	1	0	1	0	1	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
biguttatus	1	1	0	1	0	1	0	1	?	0	0	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
bimaculatus	1	1	0	0	0	2	0	0	0	0	1	?	0	1	0	0	?	?	?	?	1	0	0	0	1	0
bivestitus	1	1	0	0	0	2	0	0	0	1	1	?	0	1	0	1	?	?	?	?	1	0	1	0	0	1
bohlsi	1	1	0	0	?	2	0	1	?	1	1	?	0	?	?	?	0	0	0	0	1	0	?	0	0	1
borgmeieri	1	1	0	1	0	1	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
bruchi	1	1	0	0	0	1	?	1	?	1	1	?	0	?	?	?	0	0	0	0	1	0	1	0	0	1
chacmul	1	1	0	0	?	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	0	0	1	0
christopherseni	0	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
clypeatus	1	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	1
coffeae	1	1	0	0	0	2	0	0	0	0	1	?	0	1	0	0	?	?	?	?	0	0	0	0	1	0
columbicus	0	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
complanatus	1	1	0	0	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
conspersus	1	1	0	0	?	2	0	0	0	1	1	?	0	0	0	0	?	?	?	?	1	0	1	0	0	1
cordatus	1	1	0	1	0	1	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
cordiae	1	1	0	0	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	0
cordiventris	1	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
crenaticeps	1	1	0	0	0	2	0	0	0	0	1	?	0	1	0	0	?	?	?	?	0	0	0	0	0	1
cristatus	1	1	0	1	0	2	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
curvistriatus	1	1	0	0	0	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	0	0	1	0
decolor	1	1	0	0	1	2	1	0	0	0	1	1	0	0	0	0	?	?	?	?	0	0	0	0	0	1
decoloratus	1	1	0	0	1	2	1	0	0	0	1	1	1	0	0	0	?	?	?	?	0	0	0	0	0	1
dentidorsum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
depressus	1	1	0	1	0	1	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
duckei	1	1	0	1	0	1	0	1	?	0	0	?	0	?	?	?	0	0	0	0	0	0	0	1	0	0
ecuadorialis	?	1	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
eduarduli	1	1	0	1	0	1	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
emeryi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
femoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
fiebrigi	1	1	0	0	0	2	0	1	?	1	1	?	0	?	?	?	1	0	2	0	1	0	1	0	0	1
flavigaster	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
foliaceus	1	1	0	0	?	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	0	0	0	1
fossitborax	1	1	0	0	0	2	0	1	?	1	1	?	0	?	?	?	1	0	0	1	1	0	1	0	0	1
frigidus	1	1	1	0	0	2	0	0	1	1	1	?	0	1	0	0	?	?	?	?	1	0	1	0	0	1
goeldii	1	1	1	0	0	2	0	0	0	1	1	?	0	1	0	0	?	?	?	?	1	0	1	0	0	1
goniodontus	1	1	0	1	?	1	0	1	?	0	0	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
grandinosus	1	1	0	0	1	2	0	0	0	0	1	?	0	1	0	0	?	?	?	?	0	0	0	0	0	0
guayaki	1	1	0	0	0	2	0	1	?	1	1	?	0	?	?	?	1	0	2	0	1	0	1	0	0	1
hamulus	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
hirsutus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
inaequalis	0	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
inca	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	1	?	?
incertus	1	1	0	0	0	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	1	0	0	1
insularis	1	1	0	0	0	2	0	0	0	0	0	?	1	0	0	0	?	?	?	?	0	0	0	0	1	0
jamaicensis	1	1	0	0	1	2	1	0	0	0	1	0	0	1	0	0	?	?	?	?	0	0	0	0	0	1
jheringi	1	1	0	0	0	2	0	01	0	1	1	?	0	1	0	0	1	0	0	0	1	0	1	0	0	1
klugi	?	1	0	?	1	?	0	?	?	0	?	?	?	?	0	?	?	?	?	?	0	0	?	?	?	?
kukulcan	1	1	0	0	1	2	0	0	0	0	1	?	0	1	1	0	?	?	?	?	1	0	1	0	0	0
laminatus	0	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
laruginosus	1	1	0	0	0	2	0	1	?	1	1	?	0	?	?	?	1	1	2	1	1	0	1	0	0	1
lenca	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
liepini	1	1	0	0	1	2	0	0	0	0	1	?	0	1	1	0	?	?	?	?	0	0	1	0	0	0
liogaster	1	1	0	0	0	2	0	1	?	1	1	?	0	?	?	?	1	1	2	1	1	0	1	0	0	1
maculatus	1	1	0	0	1	2	0	0	0	1	1	?	0	1	0	0	?	?	?	?	0	0	0	0	0	1
manni	1	1	0	0	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
marginatus	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
membranaceus	1	1	0	1	0	1	0	1	?	0	0	?	0	?	?	?	0	0	0	0	0	0	0	0	0	1
minutus	0	1	0	0	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
mompox	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Tab. 3.5. Matrix of the character states among the *Cephalotes* species and four outgroups.

	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131
adolphi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
alfaroi	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
angustus	0	0	0	0	0	0	2	0	0	?	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
argentiventris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
atratus	?	?	?	?	?	1	0	?	?	?	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0
auriger	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
auricomus	?	?	?	?	?	0	0	?	?	?	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0
basalis	0	0	0	1	1	0	0	?	?	?	0	0	2	0	1	1	1	0	1	0	0	0	0	0	1	0	0
betoi	0	0	0	0	0	0	0	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
biguttatus	0	0	0	0	0	0	0	?	?	?	0	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
bimaculatus	0	0	0	0	0	0	2	?	0	?	0	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
bivestitus	0	0	0	0	0	0	2	?	1	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
boblsi	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
borgmeieri	0	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0
bruchi	0	0	0	0	0	0	1	0	?	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
chacmul	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
christopherseni	0	0	0	0	0	0	0	?	?	?	01	0	0	0	1	1	1	0	1	1	0	0	0	1	0	1	1
clypeatus	0	0	0	0	0	0	0	?	?	?	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
coffeae	0	0	0	0	0	0	2	?	0	?	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
columbicus	0	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	2	0
complanatus	0	0	0	0	0	0	0	?	?	?	0	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
conspersus	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
cordatus	0	0	0	0	0	0	1	0	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
cordiae	0	1	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	0	1	0	?	?	?	?	?	?	?
cordiventris	0	0	0	1	1	0	0	?	?	?	0	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
crenaticeps	0	0	0	0	0	0	2	?	0	?	1	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
cristatus	0	0	0	0	0	0	1	0	?	?	0	0	0	0	1	1	1	0	1	0	0	2	0	0	0	0	0
curvistriatus	0	0	0	0	0	0	2	?	0	?	0	0	2	0	1	1	1	0	1	0	0	0	1	0	0	0	0
decolor	1	0	0	0	0	0	2	?	0	0	01	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
decoloratus	1	0	0	0	0	0	2	?	0	0	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
dentidorsum	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
depressus	0	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0
duckei	0	0	0	0	0	0	1	0	?	?	0	0	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0
ecuadorialis	?	?	?	?	?	0	2	0	?	?	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
eduarduli	0	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	0	0	0	0	2	0	0	0	0	0
emeryi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
femoralis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
fiebrigi	0	0	0	0	0	0	2	1	?	?	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0
flavigaster	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
foliaceus	2	1	0	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
fossithorax	0	0	0	0	0	0	2	0	?	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
frigidus	0	0	0	0	0	0	2	?	0	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
goeldii	0	0	0	0	0	0	2	?	0	?	0	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
goniodontus	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
grandinosus	2	0	0	0	0	0	2	?	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
guayaki	0	0	0	0	0	0	2	1	?	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
hamulus	?	?	?	?	?	0	0	?	?	?	0	0	0	0	1	1	1	1	?	?	?	?	?	?	?	?	?
hirsutus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
inaequalis	0	0	1	0	0	0	0	?	?	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
inca	?	?	?	?	?	0	0	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
incertus	0	0	0	0	0	0	2	0	0	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
insularis	0	0	0	0	0	0	2	?	0	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
jamaicensis	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
jheringi	0	0	0	0	0	0	2	0	0	?	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0
kelugi	?	?	?	?	?	0	2	?	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
kukulcan	0	0	0	0	0	0	2	?	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
laminatus	0	0	1	0	0	0	0	?	?	?	0	0	1	0	1	1	1	0	1	1	0	0	0	1	0	1	1
lanuginosus	0	0	0	0	0	0	2	1	?	?	1	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0
lenca	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
liepini	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
liogaster	0	0	0	0	0	0	2	1	?	?	1	0	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?
maculatus	0	0	0	0	0	0	2	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
manni	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
marginatus	?	?	?	?	?	1	0	?	?	?	0	0	0	0	1	1	1	1	01	0	0	1	0	0	0	0	0
membranaceus	0	0	0	0	0	0	1	?	?	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
minutus	0	0	0	0	0	0	0	?	?	?	0	0	1	0	1	1	1	0	0	1	0	0	0	0	0	1	1
mompox	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Tab. 3.6. Matrix of the character states among the *Cephalotes* species and four outgroups.

	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*26*
multispinosus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
nilpiei	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1	0
notatus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	?
oculatus	0	1	2	0	1	1	0	0	1	0	0	0	1	0	2	0	1	1	0	0	1	0	1	0	0	?
opacus	0	1	2	0	1	01	0	0	1	0	0	0	1	0	2	0	1	1	0	0	1	0	1	0	0	?
pallens	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
pallidicephalus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
pallidoides	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
pallidus	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
palta	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
palustris	0	0	2	1	1	1	0	1	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
patei	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
patellaris	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
pavonii	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
pellans	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
persimilis	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
persimplex	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
peruviensis	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
pileini	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
pilosus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
pinelii	0	0	2	1	1	0	0	0	0	0	0	1	1	0	02	0	1	1	1	0	0	0	0	0	1	0
placidus	0	1	2	0	1	1	0	0	1	0	0	0	1	0	2	0	1	1	0	0	1	0	1	0	0	?
porrasi	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
prodigiosus	?	0	?	?	?	?	?	?	?	?	?	1	1	?	?	?	1	1	0	?	?	?	?	?	?	?
pusillus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	0	1	0	0	1	0	0	0	0	?
quadratus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	1	0	0	0	?
ramiphilus	0	0	2	0	1	0	0	0	0	0	0	0	1	0	2	0	1	1	0	0	0	0	0	0	0	?
resinae	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	?
robweri	0	0	2	01	1	0	0	0	0	0	0	0	1	0	2	0	1	1	1	0	0	0	0	0	0	?
scutulatus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
serraticeps	0	0	1	1	0	0	0	0	1	0	0	0	0	0	2	0	1	1	0	0	1	0	01	0	0	?
setulifer	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
simillimus	0	0	2	1	1	0	0	1	0	0	0	1	1	1	2	1	0	1	0	0	1	0	0	0	0	?
sobrius	0	0	2	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	?
solidus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	1	?	1	0	0	1	0	0	0	0	?
spinosus	0	0	2	1	1	0	0	2	0	0	0	1	1	0	2	1	0	1	0	0	1	0	0	0	0	?
supercilii	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
taino	0	0	1	1	1	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	1	0	0	0	0	?
targionii	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
texanus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
toltecus	0	0	2	1	1	0	0	0	0	0	0	0	1	0	2	0	1	1	1	0	0	0	0	0	0	?
trichophorus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
umbraculatus	0	0	2	1	1	0	0	2	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
unimaculatus	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	?
ustus	0	0	2	1	1	0	1	0	0	0	1	1	1	0	2	0	1	1	0	0	0	0	0	1	0	?
varians	1	0	2	0	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	0	?
vinosus	0	0	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	?
wheeleri	0	0	2	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	?
†alveolatus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
†bloosi	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
†brevispineus	0	0	2	1	1	0	0	0	0	0	0	1	1	?	2	1	1	1	0	0	0	0	0	0	0	?
†caribicus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	1
†dieteri	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
†hispaniolicus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
†integerrimus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
†jansei	0	0	2	0	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	01	0	0	0	0	?
†maya	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	1
†obscurus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
†olmecus	0	0	2	1	1	0	0	0	0	0	0	1	1	0	2	0	1	1	1	0	0	0	0	0	1	0
†poinari	0	0	2	1	1	0	0	0	0	0	1	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
†serratus	0	0	2	01	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	01	0	0	0	0	?
†squamosus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
†sucinus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	0	0	0	0	0	?
†ventriosus	0	0	2	1	1	1	0	0	0	0	0	1	1	0	2	0	1	1	0	0	1	0	0	0	0	?
P. belti	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	?
P. elegans	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?
P. goeldii s. l.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?
P. spiniperdus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	?

Tab. 3.7. Matrix of the character states among the *Cephalotes* species and four outgroups.

	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
multispinosus	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0
nilpiei	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
notatus	0	0	0	1	0	0	0	0	?	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	2	0
oculatus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0
opacus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
pallens	0	0	0	?	0	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0
pallidicephalus	0	0	0	1	0	0	0	0	?	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	2	0
pallidoides	0	0	0	?	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0
pallidus	0	0	0	?	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	23	0
palta	0	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	2	0
palustris	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	2	2	0
patei	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
patellaris	0	0	0	?	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
pavonii	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	2	0
pellans	0	0	0	?	0	0	0	0	?	2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0
persimilis	0	0	0	?	0	1	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
persimplex	0	0	0	?	0	1	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
peruviensis	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
pileini	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
pilosus	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
pinelii	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
placidus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
porrasi	0	0	0	?	0	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	23	0
prodigiosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
pusillus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	01	0
quadratus	0	0	0	1	0	0	0	0	?	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	2	1
ramiphilus	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	3	0
resinae	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
robweri	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0
scutulatus	0	0	0	?	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
serraticeps	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
setulifer	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
simillimus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	2	0
sobrius	0	0	0	1	0	0	0	0	?	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	2	0
solidus	?	1	0	?	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	01	0
spinosus	?	0	1	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	2	0
supercilii	0	0	0	1	0	0	0	0	?	0	1	0	1	?	0	0	0	0	0	0	1	0	0	0	2	1
taino	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
targionii	0	0	0	1	0	0	0	0	?	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	2	0
texanus	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0
toltecus	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0
trichophorus	0	0	0	1	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0
umbraculatus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	?	0
unimaculatus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
ustus	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	2	0
varians	0	0	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	12	0
vinosus	?	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	0
wheeleri	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0
†alveolatus	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
†bloosi	?	0	0	0	0	0	0	0	?	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0
†brevispineus	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	0	?	0	2	0
†caribicus	0	0	0	?	0	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
†dieteri	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
†hispaniolicus	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0
†integerrimus	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
†jansei	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
†maya	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
†obscurus	0	0	0	0	0	0	0	0	?	0	1	0	1	0	0	0	0	0	?	0	1	0	0	0	1	0
†olmecus	0	0	0	?	0	0	2	0	?	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	?	0
†poinari	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0
†serratus	0	0	0	01	0	0	0	0	?	0	01	0	0	0	0	0	0	0	0	0	1	0	0	0	01	0
†squamosus	0	0	0	01	0	0	0	01	?	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0
†sucinus	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
†ventriosus	0	0	0	1	0	0	0	0	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
P. belti	?	0	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
P. elegans	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
P. goeldii s. l.	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
P. spiniperdus	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Tab. 3.8. Matrix of the character states among the *Cephalotes* species and four outgroups.

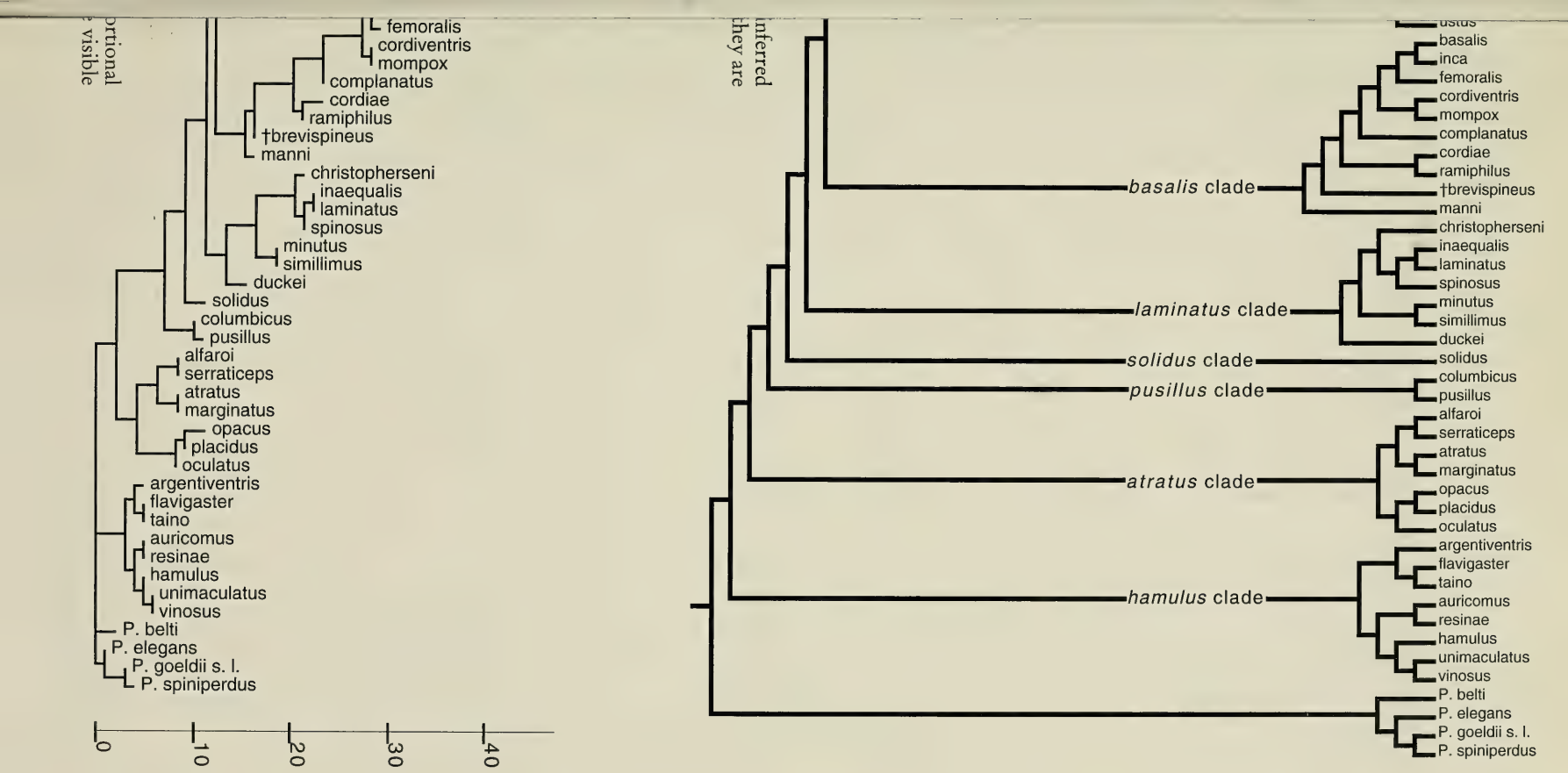
	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
multispinosus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
nilpiei	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
notatus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
oculatus	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
opacus	0	0	0	0	2	0	0	0	0	0	01	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
pallens	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
pallidicephalus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
pallidoides	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
pallidus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
palta	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
palustris	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
patei	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1
patellaris	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
pavonii	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
pellans	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
persimilis	0	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1
persimplex	0	0	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1
peruviensis	1	0	1	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	?
pileini	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
pilosus	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	1
pinelii	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
placidus	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
porrasi	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
prodigiosus	0	?	?	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
pusillus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
quadratus	0	0	0	1	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	0	1
ramiphilus	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
resinae	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	?
robweri	0	0	0	1	2	0	0	0	0	0	?	?	?	0	1	?	1	0	0	0	0	0	0	0	0	1
scutulatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
serraticeps	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
setulifer	1	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
simillimus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
sobrius	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1
solidus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
spinosus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
supercilii	0	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
taino	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	?
targionii	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	01	0	0	0	1	0	0	1
texanus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1
toltecus	0	0	0	1	2	0	0	0	0	0	?	?	?	0	1	?	1	0	0	0	0	0	0	0	0	1
trichophorus	1	0	1	1	2	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	?
umbraculatus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
unimaculatus	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	01	0	1	0	1	0	0	0	0	0	?
ustus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
varians	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
vinosus	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	?
wheeleri	0	0	0	1	2	0	0	0	0	0	?	?	?	0	1	?	1	0	0	0	0	0	0	0	0	1
†alveolatus	2	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?
†bloosi	2	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?
†brevispineus	0	0	0	?	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
†caribicus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?
†dieteri	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?
†hispaniolicus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
†integerrimus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?
†jansei	0	0	0	1	2	0	0	0	0	0	?	?	?	0	0	0	0	0	0	0	0	0	1	1	0	?
†maya	0	0	0	1	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
†obscurus	2	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?
†olmecus	0	0	0	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
†poinari	0	0	0	1	2	0	1	0	?	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
†serratus	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	?
†squamosus	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?
†sucinus	2	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	?
†ventriosus	2	0	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	1	0	0	?
P. belti	0	0	0	0	0	0	0	0	0	0	?	?	?	0	0	0	1	0	0	0	0	0	0	0	0	0
P. elegans	0	0	0	0	0	0	0	0	0	0	?	?	?	0	1	?	0	0	0	0	0	0	0	0	0	0
P. goeldii s. l.	0	0	0	0	0	0	0	1	0	0	?	?	?	0	1	?	0	0	0	0	0	0	0	0	0	0
P. spiniperdus	0	0	0	0	0	0	0	1	0	0	?	?	?	0	1	?	0	0	0	0	0	0	0	0	0	0

Tab. 3.9. Matrix of the character states among the *Cephalotes* species and four outgroups.

	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104
multispinosus	1	1	0	1	0	1	0	1	?	0	0	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
nilpiei	1	1	0	0	1	2	0	0	0	0	1	?	0	1	0	0	?	?	?	?	0	1	1	0	0	1
notatus	1	1	1	0	0	2	0	0	0	1	1	?	0	1	0	0	?	?	?	?	1	0	1	0	0	1
oculatus	1	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
opacus	?	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	0
pallens	1	1	0	0	1	2	1	0	0	0	1	0	0	0	0	0	?	?	?	?	0	0	0	0	0	1
pallidicephalus	1	1	01	0	0	2	0	0	0	1	1	?	0	1	0	0	?	?	?	?	1	0	1	0	0	1
pallidoides	1	1	0	0	1	2	1	0	0	0	1	0	0	1	1	0	?	?	?	?	0	0	0	0	0	1
pallidus	1	1	0	0	1	2	1	0	0	0	1	0	0	1	1	0	?	?	?	?	0	0	0	0	0	1
palta	1	1	0	0	?	2	0	0	0	1	1	?	0	0	0	0	?	?	?	?	1	0	1	0	0	1
palustris	1	1	0	1	?	2	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
patei	1	1	0	0	0	2	0	0	0	1	1	?	0	1	0	0	?	?	?	?	0	0	0	0	0	1
patellaris	1	1	0	0	1	2	1	0	0	0	1	0	0	0	1	0	?	?	?	?	0	0	0	0	0	1
pavonii	1	1	0	1	0	2	0	1	?	0	1	?	0	?	?	?	0	0	0	0	0	0	0	0	0	0
pellans	1	1	0	0	1	2	1	0	0	0	1	1	1	0	0	0	?	?	?	?	0	0	0	0	0	1
persimilis	1	1	0	0	1	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	0	0	0	0
persimplex	1	1	0	0	1	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	0	0	0	0
peruviensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
pileini	1	1	0	0	1	2	0	0	0	0	1	?	0	1	0	0	?	?	?	?	0	1	1	0	0	0
pilosus	1	1	0	0	0	2	0	1	?	1	1	?	0	?	?	?	1	1	2	1	1	0	1	0	0	1
pinelii	1	1	0	0	1	2	0	0	0	0	1	?	0	1	1	0	?	?	?	?	0	1	1	0	0	0
placidus	?	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
porrasi	1	1	0	0	1	2	1	0	0	0	1	0	0	0	1	0	?	?	?	?	0	0	0	0	0	1
prodigiosus	1	1	0	0	0	2	0	0	0	0	1	?	0	1	0	1	?	?	?	?	1	0	1	0	0	1
pusillus	0	1	0	0	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
quadratus	1	1	0	0	?	2	0	1	?	1	1	?	0	?	?	?	1	0	2	0	1	0	1	0	0	1
ramiphilus	1	1	0	0	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
resinae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
robweri	1	1	0	0	0	2	0	0	0	0	1	?	1	1	0	0	?	?	?	?	0	0	0	0	1	0
scutulatus	1	1	0	0	0	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	1	0	1	0	0	0
serraticeps	1	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	0
setulifer	1	1	0	0	0	2	1	0	0	0	1	0	0	1	0	0	?	?	?	?	0	0	0	0	1	0
simillimus	0	1	0	0	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
sobrius	1	1	0	0	0	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	0	0	1	0
solidus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
spinosus	0	1	0	1	0	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	1	0	0
supercilii	1	1	0	0	0	2	0	1	?	1	1	?	0	?	?	?	1	1	0	1	1	0	1	0	0	1
taino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
targionii	1	1	0	0	0	2	0	0	0	1	1	?	0	1	0	0	?	?	?	?	1	0	1	0	0	1
texanus	1	1	0	0	0	2	0	0	0	0	1	?	0	1	0	0	?	?	?	?	0	0	0	0	1	0
toltecus	1	1	0	0	?	2	0	0	1	0	0	?	1	0	0	0	?	?	?	?	0	0	0	0	1	0
trichophorus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
umbraculatus	1	1	0	1	0	2	0	0	0	0	1	?	0	0	0	0	?	?	?	?	0	0	0	0	0	1
unimaculatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ustus	1	1	0	1	?	0	?	?	?	?	?	?	0	?	?	?	?	?	?	?	0	0	0	0	0	0
varians	1	1	0	0	1	2	1	0	0	0	1	0	0	1	0	0	?	?	?	?	0	0	0	0	0	1
vinosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
wheeleri	1	1	0	0	?	2	0	0	1	0	0	?	1	0	0	0	?	?	?	?	0	0	0	0	1	0
†alveolatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†bloosi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†brevispineus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†caribicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†dieteri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†hispaniolicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†integerrimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†jansei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†maya	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†obscurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†olmecus	1	1	0	0	?	2	0	0	0	0	1	?	0	?	0	0	?	?	?	?	0	0	0	0	0	?
†poinari	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†serratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†squamosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†sucinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†ventriosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. belti	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?
P. elegans	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. goeldii s. l.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. spiniperdus	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?

Tab. 3.10. Matrix of the character states among the *Cephalotes* species and four outgroups.

	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	129	130	131
multispinosus	0	0	0	0	0	0	1	0	?	?	0	0	2	0	1	1	1	0	1	0	0	0	0	0	0	0	0
nilpiei	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
notatus	0	0	0	0	0	0	2	?	0	?	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
oculatus	?	?	?	0	?	0	0	?	?	?	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0
opacus	0	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0
pallens	1	0	0	0	0	0	2	?	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
pallidicephalus	0	0	0	0	0	0	2	?	0	?	0	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
pallidoides	1	0	0	0	0	0	2	?	0	0	?	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
pallidus	1	0	0	0	0	0	2	?	0	0	?	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
palta	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
palustris	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
patei	0	0	0	0	0	0	2	?	0	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
patellaris	1	0	0	0	0	0	2	?	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
pavonii	0	0	0	0	0	0	1	0	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
pellans	1	0	0	0	0	0	2	?	0	0	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0	0	0
persimilis	12	0	0	0	0	0	2	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0
persimplex	2	0	0	0	0	0	2	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
peruviensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
pileini	0	0	0	0	0	0	2	?	0	0	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
pilosus	0	0	0	0	0	0	2	1	?	?	0	0	1	0	1	1	1	0	01	1	0	0	0	0	0	0	0
pinelii	0	0	0	0	0	0	2	?	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
placidus	?	?	?	0	?	0	0	?	?	?	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0
porrasi	1	0	0	0	0	0	2	?	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
prodigiosus	0	0	0	0	0	0	2	?	1	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
pusillus	0	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	0	1	1	0	0	0	1	0	2	0
quadratus	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
ramiphilus	0	1	0	0	0	0	0	?	?	?	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?
resinae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
robweri	0	0	0	0	0	0	2	?	0	?	0	0	0	0	1	1	1	0	?	1	0	0	0	0	0	0	0
scutulatus	0	0	0	0	0	0	2	?	0	?	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0
serraticeps	0	0	0	0	0	0	0	?	?	?	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
setulifer	0	0	0	0	0	0	2	?	0	?	0	0	2	0	1	1	1	0	1	0	0	0	0	0	0	0	0
simillimus	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
sobrius	0	0	0	0	0	0	2	?	0	?	0	0	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?
solidus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
spinosus	0	0	1	0	0	0	0	?	?	?	0	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
supercilii	0	0	0	0	0	0	2	1	?	?	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
taino	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
targionii	0	0	0	0	0	0	2	?	0	?	0	0	1	0	1	1	1	0	?	0	0	0	0	0	0	0	0
texanus	0	0	0	0	0	0	2	?	0	?	0	0	2	0	1	1	1	0	?	0	0	0	1	0	0	0	0
toltecus	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
trichophorus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
umbraculatus	0	0	0	1	0	0	2	0	0	?	0	0	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0
unimaculatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	0	1	0	0	0	0	0	0
ustus	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
varians	0	0	0	0	0	0	2	?	0	0	0	0	0	0	1	1	1	0	01	0	0	0	0	0	0	0	0
vinosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
wheeleri	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†alveolatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†bloosi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†brevispineus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†caribicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†dieteri	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†hispaniolicus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†integerrimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†jansei	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†maya	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†obscurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†olmecus	2	1	0	?	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†poinari	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†serratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†squamosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†sucinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†ventriosus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. belti	?	?	?	?	?	0	0	?	?	?	0	0	0	0	0	0	0	1	0	?	?	?	?	?	?	?	?
P. elegans	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. goeldii s. l.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	0	0	0	0	0	0	0
P. spiniperdus	?	?	?	?	?	0	0	?	?	?	0	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?


ortional
visible
inferred
they are
femoralis
cordiventris
mompox
complanatus
cordiae
ramiphilus
†brevispineus
manni
christopherseni
inaequalis
laminatus
spinosus
minutus
simillimus
duckei
solidus
columbicus
pusillus
alfaroi
serraticeps
atratus
marginatus
opacus
placidus
oculatus
argentiventris
flavigaster
taino
auricomus
resinae
hamulus
unimaculatus
vinosus
P. belti
P. elegans
P. goeldii s. l.
P. spiniperdus
0
10
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basalis clade
laminatus clade
solidus clade
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hamulus clade
basalis
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femoralis
cordiventris
mompox
complanatus
cordiae
ramiphilus
†brevispineus
manni
christopherseni
inaequalis
laminatus
spinosus
minutus
simillimus
duckei
solidus
columbicus
pusillus
alfaroi
serraticeps
atratus
marginatus
opacus
placidus
oculatus
argentiventris
flavigaster
taino
auricomus
resinae
hamulus
unimaculatus
vinosus
P. belti
P. elegans
P. goeldii s. l.
P. spiniperdus

Fig. 24. Facing page 80. - Unique most parsimonious cladogram for the 131 known species of *Cephalotes* fossil and extant. The cladogram has been inferred heuristically from the characters tabulated in Tab. 3. The labels on the vertical branches indicate the more homogeneous and distinct clades as they are defined in the text.

Branch lengths proportional to
Chars. that change
Unambiguously on branch

Fig. 25. Facing page 80. - Same *Cephalotes* phylogeny as in Fig. 24 expressed as a phylogram in which the lengths of the different branches are proportional to the number of synapomorphies characterising each branch. Autapomorphic characters have been excluded from the data matrix and the visible species-level apomorphies result from secondary losses or homoplastic gains of otherwise synapomorphic characters.

The presence or absence of these characters among the *Cephalotes* species we recognise, fossil and extant, is given in Table 3.

Given the probable high degree of convergence or parallelism among most characters we already mentioned, for the phylogenetic analysis, character evolution has been assumed to be always unordered.

5.5. Tentative reconstruction of the *Cephalotes* phylogeny

Probable synapomorphies within *Cephalotes* have been inferred by outgroup comparison. According to the results of our former genus-level analysis, we choose as outgroup(s) exclusively members of the sister-genus *Procryptocerus*. These comprise the following three species chosen as to encompass most of the observable *Procryptocerus* diversity: *P. belti* FOREL from Central America, *P. spiniperdus* FOREL from Trinidad, and *P. elegans* SANTSCHI from Brazil. Since males suitable for dissection were not available for any of these species (the male of *P. elegans* is still unknown) and since, in our analysis, we made use of internal genitalic structures, we added also another outgroup species of which we have been able to perform dissections, i. e. a *Procryptocerus* nest series with abundant males from Botucatu (São Paulo, Brazil) probably referable to *P. goeldii* FOREL or to some of its subspecies.
We performed nine heuristic searches for the shortest tree(s) computable from our data of Table 3 as described in the methods chapter with the following results:
1. Addition sequence of species simple, branch swapping by tree bisection-reconnection : 124 trees of length 701.
2. Addition sequence of species simple, branch swapping by subtree pruning-regrafting: 1 tree of length 697.
3. Addition sequence of species simple, branch swapping by nearest-neighbour interchanges: 10,000 (i. e. our MAXTREES limit) trees of length 720.
4. Addition sequence of species closest, branch swapping by tree bisection-reconnection: 122 trees of length 701.
5. Addition sequence of species closest, branch swapping by subtree pruning-regrafting: 1 tree of length 697, identical to the tree found during search # 2.
6. Addition sequence of species closest, branch swapping by nearest-neighbour interchanges: 405 trees of length 703.
7. Addition sequence of species random, branch swapping by tree bisection-reconnection (10 replicates): 1 tree of length 697 (found in six replicates), identical to the tree found during search # 2.
8. Addition sequence of species random, branch swapping by subtree pruning-regrafting (10 replicates): 1 tree of length 697 (found in eight replicates), identical to the tree found during search # 2.
9. Addition sequence of species random, branch swapping by nearest-neighbour interchanges (number of replicates originally set to 10): 10,000 trees (i. e. our MAXTREES limit) of length 699 stored after the first replicate. Search terminated prematurely (no room to store new trees).

We retained, hence, this single tree of length 697 (Fig. 24, see folding page) as optimal. The same tree had been already found during earlier heuristic searches performed on the same data matrix and starting from previously supposed optimal trees resulting from slightly different data matrices.

Since autapomorphies had been excluded from the data matrix all characters resulted cladistically informative and the length and fit measures of the former unique shortest tree are the following: Tree Length 697, CI = 0.525, HI = 0.601, RI = 0.865, RC = 0.454.

Fig. 25 (see folding page) is based on the same data as Fig. 24 but it is expressed as phylogram, i. e. the length of the different branches is proportional to the number of synapomorphies justifying them.

The great degree of homoplasy and the resulting low consistency already hypothesised from the adaptive significance of most characters on which the analysis was based are rendered evident from the length of our tree after assigning equal weight = 1 to all characters (TL 373 with 131 characters) and from the aforementioned measures of characters' fit on this tree.

In order to have a first rough test of the reliability of our tree we evaluated the length of 10,000 trees sampled randomly from the set of all possible trees drawn from our data matrix. The mean length of these trees is 2578 (SD = 32) with a unique shortest tree of length 2426 (max. 2668).

Computation of FAITH & CRANSTON's (1991) permutation tail probability, as one might have expected, gave very similar results: 99 data matrices permuted as described in the methods chapter allowed the evaluation of 99 (sets of) trees with a mean length of 2003 (SD = 15) and with the shortest tree(s) of length 1922, pointing out in this way a high degree of cladistic covariation of our data.

The bootstrap analysis performed as described in the Methods chapter, however, gave much less satisfactory results. Only three major clades appeared in frequencies superior to the conventional statistical limits of significance (those which in Chapter 5 will be named as *hamulus* clade, *clypeatus* clade and *wheeleri* clade). Otherwise, the resulting tree (drawn allowing minority compatible groupings to be retained) has a length of 721 and shows some topological differences with our most parsimonious tree. We explain in part this result by the numerical inadequacy of our analysis since the maximum number of trees retained (10,000) is still too small, and, of course, the number of presumable synapomorphies on which the analysis is based is objectively insufficient to draw a steady phylogeny from a data matrix with 135 taxa and 131 characters. For these reasons we thought it better not to reproduce at all the bootstrap-derived tree.

If, on one hand, we are sure that our tree is destined to further improvement and modification when additional information will be available, on the other hand we are not dissatisfied with it. The reasons of our complacency are the following:

1. Two explorative analyses of the same data matrix by means of distance measures and cluster analysis resulted in not too different trees containing most sets of species identified as the major clades in this paper.

2. The major clades appearing in our unique optimal tree correspond largely to the species groups intuitively recognised by KEMPF (1951) and to those that we had expected to find according to our experience with the species in question. When the results of our analysis differed from our expectation we had to admit the superiority of the rationale of the computing algorithm over our intuition.

We must stress, at this point, that we consider our former conclusions about the generic classification of the Cephalotini as correct, though we are aware of the fact that our main accomplishment has been demonstrating the failures of the previous classification by means of a sound logical analysis applied to unsound data.

In fact, extrapolating part of the results obtained from the species-level analysis, the most probable phylogeny of all the species involved shows that *Zacryptocerus*, as it is currently understood and as we included it in our genus-level analysis, is a paraphyletic group according to all fashionable definitions of the term available from the literature, since (i) there is no unique common ancestor for all its members and only for them (HENNIG, 1950), (ii) it does not contain all the descendants of the most recent common ancestor (ASHLOCK, 1971), (iii) it includes a common ancestor and only part of its descendants (NELSON, 1971; FARRIS, 1974).

We already said that the genus-level treatment of the Cephalotini is greatly affected by the lack of convincing synapomorphies for the former genus *Hypocryptocerus*. As a matter of fact we have some circumstantial evidence that at least one such synapomorphy may be found by using biochemical characters: *Cephalotes auricomus* (the sole "*Hypocryptocerus*" species with which we have field experience) is very characteristic for producing a strong smell of decaying citrus, a smell indistinguishable among all other *Cephalotes* species with which we are acquainted. Given the great morphological similarity of all "*Hypocryptocerus*" species one would expect the production of this pheromone to be synapomorphically shared by all of them; if the absence of this compound among the remaining *Cephalotes* species could be reasonably proved, we think that at least *Hypocryptocerus* should be resurrected as a valid genus.

On the other hand, the most parsimonious tree resulting from our study shows that the phylogenetic relationships of the older genera now included in *Cephalotes* corresponds well to the intuition of the former students dealing with these ants (see e. g. WHEELER, 1920 and KEMPF, 1951) and it is as follows:

(*Hypocryptocerus*, ((*Cephalotes* + *Eucryptocerus*), (remaining *Zacryptocerus*))).

The sole reason for which we do not re-propose the older generic classification or a slight modification of it relies on the lack of (known) strong synapomorphies for most of these clades. At the present state of knowledge, in our tree of Fig. 24, the involved clades representing former putative genera can be characterised by means of synapomorphic traits of unequal phylogenetic significance as they are listed in the following:

Hypocryptocerus

1. Vertexal angles round and superficially crenulate. This is a unique trait but we are reluctant to attribute it generic value because of the non-generic bewildering array of vertexal morphologies to be found in other, presumably related, species. In addition, the *Hypocryptocerus* morphology is not too dissimilar from the one of the members of the distantly related *wheeleri* clade.

2. Lateral petiolar spines shorter than 1/3 of the maximum petiolar length. This character state is synapomorphic for *Hypocryptocerus* since it is absent among both most adjacent clades. The same morphology is widespread among several distantly related *Cephalotes* species.

3. Extensor face of tibiae with longitudinal striation. This character is also present homoplastically in the distantly related species *rohweri* and in a number of *Procryptocerus*.

Remaining *Cephalotes* except *Hypocryptocerus*

1. Loss or transformation of the body covering of abundant, truncate hairs. This character is not constant since abundant truncate hairs reappear in far, terminal species like *wheeleri* and *fiebrigi*.

2. Secondary loss of the striation of the ventral face of the head, a weak character since the striation reappears homoplastically among some terminal species of the clade like *curvistriatus* and *lenca*.

Cephalotes s. str. + *Eucryptocerus*

1. Vertexal angles bispinose. This appears as a good synapomorphy for this clade. A few outgroup species (e. g. *borgmeieri*, *cristatus*) have bidenticulate vertexal angles but the two morphologies are hardly comparable.

3. Presence of dorsal pronotal spines. A character unique to this clade but missing e. g. in small workers of *atratus*, *alfaroi*, *serraticeps* and *opacus*.

As one can see from the previous list of synapomorphies, the generic status of *Cephalotes* s. str. could still be reasonably defended on the basis of the bispinose vertexal angles but this course of action would result in the paraphyly of *Zacryptocerus* as already discussed in the previous pages.

Remaining *Zacryptocerus*

1. Presence of a hypostomal bridge. The hypostomal bridge, widespread among most species of the clade, is absent in most members of the *basalis* clade and of the *wheeleri* clade.

2. Anterior coxae protruding forwards. This character is present, to various extents, in most species of the clade but it appears to be missing at least in *C. cordiae*.

3. Presence of the soldier caste. This, apparently excellent, character is strongly weakened by the presence of soldiers in three species of the sister clade, the *atratus* clade. Since the majority of the species of the *atratus* clade don't have a soldier caste, our phylogenetic reconstruction assumes that the soldier caste arose three times independently among *Cephalotes* (see also Fig. 377).

4. Basal face of the propodeum plate-like and followed by a spine. This is a character quite regularly present among the basalmost species of the clade (except *cordiae*) but absent among the majority of its members.

5. Male propodeum unarmed. This character is constant among all the males of the clade known so far (41 species). Its value is weakened by the fact that the male propodeum is unarmed in one closely related outgroup species (*serraticeps*) and polymorphic in another (*atratus*).

From all the previous considerations it follows that, at the present state of knowledge, the sole resulting monophyletic clade characterised by apomorphies of probable generic value is the one containing the former genera *Cephalotes* (s. str.) and *Eucryptocerus*. On the other hand, the individual generic status of this clade can not

be maintained since this will automatically imply generic significance for its sister group and outgroup clades, two clades for which important, unequivocal synapomorphies are missing or still unknown.

5.6. Principal clades and constituent species

In the following we provide a list and short descriptions of all known *Cephalotes* species. Our specific treatment should not be regarded as a true monograph nor as a revision. We made no serious efforts to describe all the undescribed species probably already available in several museum collections and even less to discover new species in the field. The sole exceptions to this principle are represented by two short trips by M. L. DE ANDRADE, one to the Dominican Republic with the only target to discover the first gyne and to confirm the previously supposed absence of soldiers among species of the *hamulus* clade and another to the Amazon to collect fresh material of some critical species. As already stated in the introduction, the main goal of the present paper is to propose a reasonable phylogenetic placement and interpretation of the fossil species. During our work, of course, we encountered several species-level taxonomic problems that we tried to solve, some undescribed Recent species which will be described here for the first time, and significant new material for species incompletely known until now which we included in our analysis. Nonetheless, a great proportion of the species to be included in this chapter has been already described and figured in an exhaustive, reliable way in one or another study on the Cephalotini by KEMPF (1949–1974) who gives also complete synonymies and lists of localities. Since most of these descriptions are very accurate and still valid, here we will report them entirely (plus a few more by others) in order to facilitate the task of potential interested readers. We thought it redundant and immodest from our side to rewrite with our words parts of information which are already available as a result of somebody else's research.

An exhaustive synonymy for all the species treated in this paper can be found in the aforementioned papers by KEMPF (1949–1974) and the latest ones have been added in the catalogues by BRANDÃO (1991) and BOLTON (1995 b). We refer to these works for most established synonyms of the species considered by us. Also the synonymies accompanying our species treatment, hence, have been reduced to the essential or to the citation of papers relevant for our purpose and not considered in the previous monographs.

As a result of the generic synonymies we propose in this paper several new combinations which will be introduced for species currently included in *Zacryptocerus*, *Eucryptocerus*, *Exocryptocerus* and now transferred to *Cephalotes*. As a matter of fact, the majority of these binomina in *Cephalotes* appear already in the catalogue of BOLTON (1995 b, pp. 140–142). We do not regard the publication of these binomina in this context as the first transfer of these species to *Cephalotes* because (i) the purpose of this procedure is declared to be a search facility and not a nomenclature change (see BOLTON, l. c., p. 52), and, (ii) immediately after the first appearance of a species name in *Cephalotes* the same species is referred again to another genus (most of them to *Zacryptocerus*) where the complete treatment of the species is to be found.

The pre-existence of the aforementioned, important monographs greatly facilitated our task and we regard the set of synapomorphy hypotheses already listed under Chapter 5.4 and allowing a tentative phylogenetic arrangement of the species as our main original contribution to the knowledge of *Cephalotes*.

5.6.1. The *hamulus* clade

This clade corresponds to the former genus or subgenus *Hypocryptocerus* and contains all the less specialised species of the genus *Cephalotes*. It is characterised by only three synapomorphies: (1) the vertexal angles broad, round and with crenulate margin, (2) the outer face of tibiae with longitudinal, irregular rugae, a character shared homoplastically also with the far relative *rohweri* (a member of the phylogenetically distant *wheeleri* clade) and with some species of the sister genus *Procryptocerus*, and, (3) petiolar spines present but shorter than 1/3 of the petiolar length, a character re-appearing in a number of distantly related, more specialised *Cephalotes* species. We regard this as an additional demonstration of the inappropriateness of considering *Hypocryptocerus* as a valid genus. We shall name the species of this group as *hamulus* clade for uniformity with other, comparable, phyletic lines we recognise within *Cephalotes*. Since the name *Hypocryptocerus* already exists in the literature, there are, however, no serious reasons against the use of this name as a subgeneric name for those preferring this formal solution.

Practically, if one disposes of abundant *Cephalotes* nest series, he should be able to recognise the members of the *hamulus* clade at glance by their possibly unique possession of one very important plesiomorphy: the absence of soldiers and the monomorphism of the worker caste, a character state unknown in other *Cephalotes* (though it may be present in the poorly known species *placidus* and *oculatus* in the *atratus* clade), but which is the rule among the species of the sister genus *Procryptocerus*.

Within the *hamulus* clade we recognise eight valid species and a possible, insufficiently known, ninth species is listed in Chapter 5.7. All these species are presumably endemic on the Island of Hispaniola and two of them are known only from copal samples of probable historical age. One could expect to encounter them again in the Recent fauna of the island.

A circumstance apparently contrasting with the antiquity of the clade is that its members are very similar each other and are likely to be the product of relatively young speciation events, a hypothesis supported also by palaeogeographic evidence (see later, Chapter 7). The main diagnostic characters among them appear to be confined to integumental sculpture, pilosity and coloration. As a result of this situation, the internal phylogeny of the clade is far from being properly understood and, due to our incapacity to detect sufficient, plausible synapomorphies, the internal phylogeny of this clade as drawn in Fig. 24 should be considered as tentative. The known members of the *hamulus* clade are listed and discussed in the following.

Species included in the clade: *argentiventris*, *auricomus*, *flavigaster*, *hamulus*, *resinae*, *taino*, *unimaculatus*, *vinosus*.

Cephalotes hamulus (ROGER) bona species, new combination

Fig. 26

Cryptocerus hamulus ROGER, 1863: 209. Worker. Original description. Type locality: Santo Domingo. Type material: one syntype worker labelled "*Cryptc. hamulus*, S. Domingo, Type" in the MCSN, examined. Additional syntype workers presumably in the "Zoologisches Museum an der Humboldt-Universität", Berlin.

Cryptocerus haemorrhoidalis (LATREILLE), WHEELER & MANN, 1914: 38, fig. 16 (nec LATREILLE, 1802 b). Worker, male. Misidentification proposed by WHEELER, 1936 b: 201.

Cryptocerus hamulus var. *haytianus* (sic) FOREL, 1901 b: 337. Worker. Original description. Type locality: Haiti. Type material: 2 probably syntype workers labelled "Cr. h. haytianus, Haiti" in MHNG (examined). Synonymy by WHEELER, 1936 b: 201.

Hypocryptocerus haemorrhoidalis hamulus (ROGER), WHEELER, 1936 b: 201. First combination in *Hypocryptocerus*.

Hypocryptocerus haemorrhoidalis hamulus (ROGER), KEMPF, 1951: 149. Worker and male.

Hypocryptocerus haemorrhoidalis affinis WHEELER, 1936 b: 202. Worker. Original description. Type locality: Poste Terre Rouge (Haiti). Type material: 2 syntype workers in the MCZC (KEMPF, 1951: 147), examined. N e w s y n o n y m .

?*Zacryptocerus haemorrhoidalis*, KUGLER, 1978: 474, figs. 198–199. Worker, sting.

Zacryptocerus haemorrhoidalis hamulus (ROGER), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *hamulus* clade characterised by the following apomorphies: completely black body with longitudinal rugosities on the anterior fourth of the first gastral tergite and thin, short, appressed hairs on the gaster.

W o r k e r (Fig. 26). - Vertexal angles round, with crenulate margin; vertexal margin gently concave medially. Vertex with a median pair of small denticles and a trace of transverse carina. Frontal carinae reaching the middle of the eyes posteriorly, their sides expanded, not completely covering the cheeks. Cheeks posteriorly marginate. Anterior clypeal border concave in the middle and bearing two small lateral teeth. Eyes gently convex. Mandibles without lateral carinae, robust, and directed ventrally; the masticatory margin with a developed apical followed by a smaller preapical tooth and by 0–4 minute denticles or by an edentate margin.

Mesosoma robust, slightly convex in side view. Scapular angles bearing a pair of small denticles. Anterior pronotal border variably marked by a carina. Humeral angles with a pair of obtuse or stout spines directed anteriorly. Pronotal sides straight, ending in a small tooth visible in dorsal view. Promesonotal suture impressed laterally, more superficial in the middle of the dorsum. Mesonotal teeth small, obtuse or round or absent. Propodeal suture deeply impressed dorsally. Propodeum with differentiated basal and declivous faces. Basal face slightly more than 1/3 broader than long, with convex or obtuse sides anteriorly, straightening posteriorly and with or without a small denticle; declivous face as long as the basal face, with posteriorly slightly converging sides. Propodeal spines subequal to the basal face of the propodeum, thick and diverging.

Petiole ca. 1/2 broader than long, its anterior face truncate and slightly concave; its sides converging posteriorly, bearing a pair of anterior denticles and a pair of pointed teeth medially, both variable in size. Postpetiole broader than and as long as the petiole; postpetiolar spines broad and variably pointed, inserted anteriorly and curved backwards.

Gaster with a membranaceous anterior crest, broad in most specimens, and reaching the first gastral stigma at maximum.

Legs. Fore coxae without a broad lobe or angle anteriorly. Hind femora slightly inflated in the middle; mid and hind basitarsi laterally compressed; their sides narrowing distally in side view.

Sculpture. Head minutely reticulate; vertexal area covered by broad impressions or irregular foveae gradually shallower towards the cheeks, sparser and small anteriorly. Frontal carinae reticulate and faintly rugulose on their sides. Ventral part of the head laterally covered by thick, regular striae. Hypostomal area deeply reticulate. Cheeks reticulate and rugulose on their posterior half.

Mesosoma, petiole and postpetiole covered by dense, longitudinal, irregular rugae, and by superficial, minute reticulation. The striae more regular on the pleurae. Declivous face of the propodeum partially or entirely covered by superficial to thick, longitudinal rugae, and reticulation variably impressed.

First gastral tergite reticulate, with longitudinal rugosities on its anterior fourth and on its ventral marginal area. Corresponding sternite with superficial longitudinal rugosities on the sides, the rest with impressed reticulation and opaque, or faintly reticulate and slightly shining in the middle, and with sparse piligerous foveae.

Coxae with sparse, transversal or longitudinal rugosities and reticulate. Femora deeply reticulate and with sparse, thin, irregular, transversal rugae variably impressed; dorsally with a pair of distal, short, carinae more impressed on the mid and hind legs. Outer face of tibiae and basitarsi with longitudinal, slightly anastomosing rugosities, otherwise reticulate.

Pilosity. Body with the following types of hairs: (1) truncate, erect to suberect, long on the vertexal area, on the mesosoma and on the pedicel, shorter on the anterior part of the head, on the gaster and legs; (2) thick and appressed, long on the vertexal area, on the mesosoma and pedicel; (3) thick, short, sparse, appressed on the anterior half of the head, thinner on the gaster and on the legs; (4) thin, very long and pointed on the sternites.

Colour. Black. Frontal carinae, scapes and tarsomeres dark orange to light brown. Vertexal area, mesosoma and pedicel with some golden reflexes.

Measurements (in mm) and indices: TL 6.16–7.16; HL 1.46–1.68; HW 1.68–1.96; EL 0.44–0.52; PW 1.52–1.80; PeW 0.72–0.86; PpW 0.96–1.08; HBaL 0.68–0.76; HBaW 0.16–0.20; CI 114.6–116.6; PI 108.8–111.3; PPeI 200.0–233.3; PPpI 158.3–175.0; HBaI 23.5–26.3.

G y n e (previously undescribed, tentative specific attribution). - Differing from *auricomus* in the following characters: head less convex, vertexal angles convex and broader. Vertex with a longer pair of median denticles and with the transversal carina more impressed.

Mesosoma. Humeral angles with a pair of longer anterior teeth. Pronotal crest strongly marked by a row of higher, pointed denticles.

Petiole with the anterior face separate from the posterior one by a visible carina interrupted medially. Postpetiole and gaster missing.

Legs. Fore coxae without a broad lobe or angle anteriorly. Hind femora slightly inflated in the middle; mid and hind basitarsi laterally compressed; their sides narrowing distally in side view.

Sculpture. Vertexal area superficially reticulate, irregularly foveolate-rugulose, the foveae more regular and small anteriorly. Ventral side of the head punctate and covered by thick, regular striae. Cheeks reticulate and irregularly rugose.

Mesosoma and petiole reticulate and covered by thick, irregular foveae and rugosities, the rugosities more longitudinally oriented on the mesonotum, scutellum, propodeum and petiole. Lower mesopleurae and metapleurae reticulate and with thin rugosities, the rugosities more regular and sparser on the metapleurae. Declivous face of the propodeum reticulate and with short rugosities on the middle only: longitudinal superiorly and transversal inferiorly.

Legs reticulate; outer face of the tibiae with thin, irregular, longitudinal rugosities.

Pilosity. Body with the following types of hairs: (1) truncate, erect to suberect, long on the vertexal area, on the mesosoma and on the petiole, shorter on the anterior part of the head and on the legs; (2) thick and decumbent, long on the vertexal area, on the mesosoma and petiole, shorter on the anterior half of the head, dense on the middle of the basal face of the propodeum; (3) thin, short, sparse, appressed on the legs.

Colour. Black. Frontal carinae and antennae dark orange-ferrugineous. Body with silvery reflexes given by the pilosity.

Measurements (in mm) and indices: TL (gaster missing in the unique specimen; length of the gaster measured on the complete print left in the glue) ~9.18; HL 1.96; HW 2.12; EL 0.56; PW 2.08; PeW 0.76; HBaL 0.76; HBaW 0.22; CI 108.2; PI 101.9; PPeI 273.7; HBaI 28.9.

Male (description of Kempf, 1951). - "Head, thorax, coxae, peduncle fuscous brown. Legs, tips of mandibles, scape and gaster yellowish brown. Funiculus light brown. Mandibles with a distinct apical and preapical tooth; the following teeth vestigial. Head transverse; the median head length shorter than the interocular width. Frontal carinae divergent, fading out above the eyes. Antennal scrobe obsolescent. Eyes large, their maximum diameter subequal to half of the median head length. Occiput evenly rounded transversely without forming distinct lateral angles. Integument finely reticulate-punctate. Transverse rugae between the upper border of the eyes and the front. Scape about half as long as the second funicular segment. Sides of pronotum diverging behind, with a distinct scapular tooth. A vestigial transverse carina across the pronotum. Laterotergite excavated beneath just above the fore coxae. Scutum and scutellum considerably convex. Mayrian furrows deeply impressed. Upper mesopleura strongly convex.

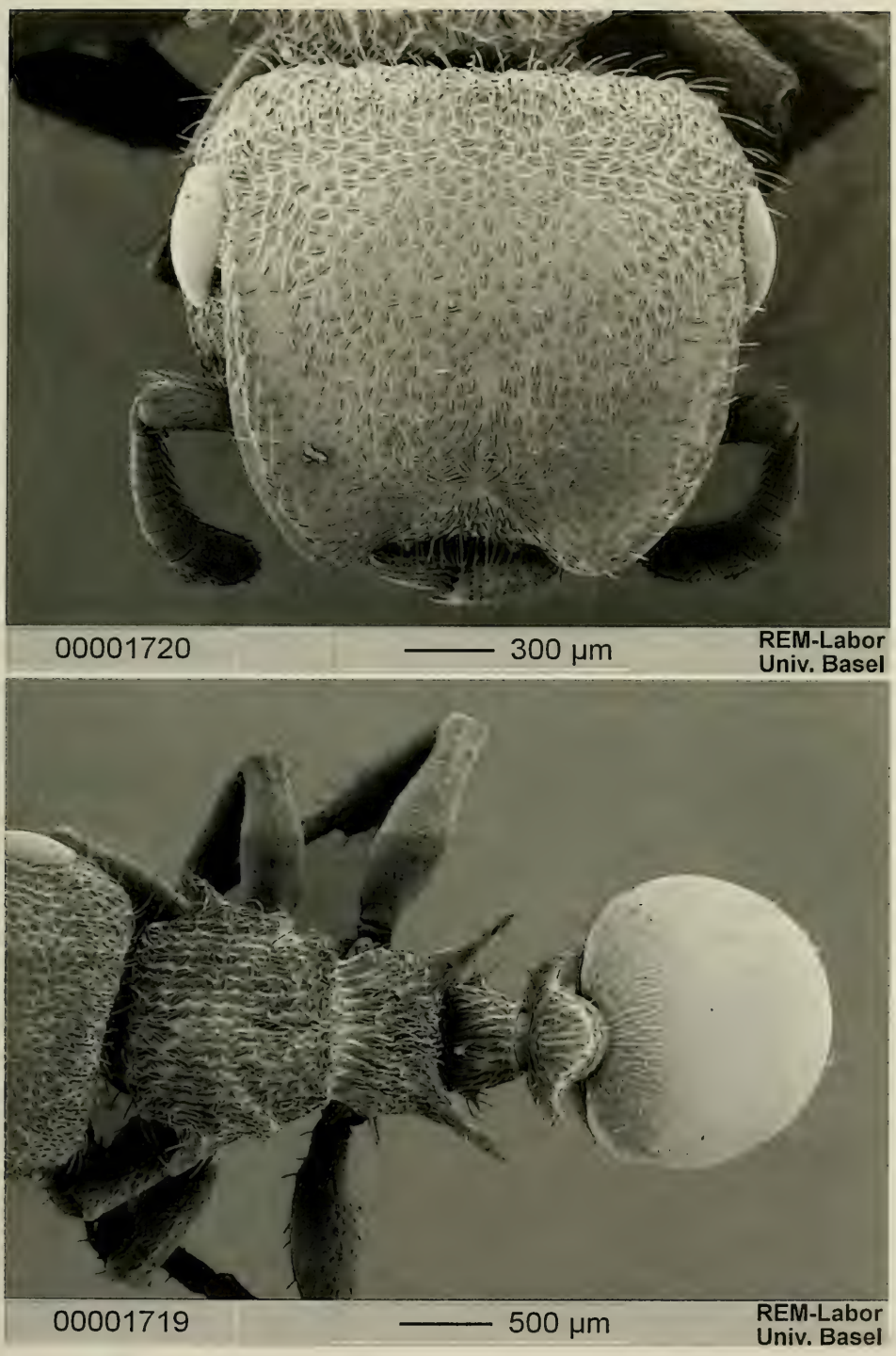


Fig. 26. *Cephalotes hamulus* (ROGER). Worker from Jarabacoa, Dominican Republic: head (top) and mesosoma (bottom) in dorsal view.

Epinotum transverse, the posterior corners of the basal face dentate. Integument finely reticulate-punctate, irregularly rugulose. Petiole about as long as wide, with a vestigial tooth on each side. Postpetiole flat above, subquadrate, with a tubercular tooth on each side. Gaster finely reticulate, subfulgid. The genitalia have been lost. Pile (sic) fulvous and erect, abundant and conspicuous on head and thorax; sparser and appressed on gaster and legs. Wings slightly infumated; veins brunneous. Fore wing with a closed and appendiculate marginal cell, and a transverse cubital vein. Submarginal cell short. Transverse median vein about half as long as the second abscissa of the median vein."

Note: the sole known male of this species in the MCZC lacks the last 6 gastral segments and the genitalia as already mentioned by KEMPF (1951).

Measurements (in mm) and indices: TL 5.62 (excluding gastral segments 2–8 missing in the only available specimen); HL 0.94; HW 1.16; EL 0.46; PW 11.08; PeW 0.48; PpW 0.52; HBaL 0.85; HBaW 0.11; CI 123.4; PI 107.4; PPeI 225.0; PPpI 207.7; HBaI 12.9.

Material examined. - **Haiti**: no further locality, 1 gyne [MNHN]; idem, 2 workers (probable syntypes of *hamulus haytianus*) [MHNG]; Diquini, 1 worker, W. M. MANN [NHMB]; Mts. N of Jacmel, 10 workers, W. M. MANN [MCZC, MZSP, NHMB]; Manneville, 2 workers, W. M. MANN [MCZC]; Port au Prince, 4 workers and 1 male, W. M. MANN [MCZC, NHMB]; Port au Prince, 1 worker, 06.XII.1901, G. KELTEL [MHNG]; unintelligible locality, 1 worker, [MHNG]; Porte Terre Rouge, 2000', 05.X.1934, 2 workers (syntypes of *affinis*) [MCZC].
Dominican Republic: S. Domingo (no further data, syntype of *hamulus*), 1 worker, [MCSN]; Prov. La Vega, 12 km NE Jarabacoa, 550 m, 02.X.1988, pine forest, 2 workers, M. A. IVIE, T. K. PHILIPS & K. A. JOHNSON [USNM].

Discussion. - *C. hamulus* is recognisable by its completely black body with the anterior fourth of the first gastral tergite completely or partially covered by longitudinal rugosities. It results as outgroup of the sister species *resinae* and *auricomus*. The three species share the pilosity completely or partially hiding the sculpture.

This and a number of other taxa of the *hamulus* clade were formerly regarded as subspecies of *C. haemorrhoidalis*, a species which can not be identified with certainty at present (see chapter 5.7, *Cephalotes* incertae sedis). Due to the close sympatry and apparent lack of transitional forms between most of these nominal taxa, in this paper, we consider a number of them worthy of specific rank. This is the case with *hamulus*. We named the whole clade after this species since it is the oldest described taxon in the clade which corresponds to a still identifiable species (due to the availability of type material).

C. haemorrhoidalis affinis WHEELER, described on two workers only (examined) has been separated on minute sculptural and morphological differences of the propodeum and of the pedicel which appear to be variable and inconsistent within the material available for the present study. Here it has been considered as a synonym of *hamulus* as KEMPF (1951) already suspected.

We tentatively attribute a gyne from Haiti (MNHN) without postpetiole and gaster to *hamulus* for the following reasons: (1) there are three species of the *hamulus* clade known from Haiti, i. e. *hamulus*, *vinosus* and *unimaculatus*; (2) gynes are systematically larger than workers, (3) the measurements of the Haitian gyne are larger than those of *hamulus* workers but within the range of *vinosus* and *unimaculatus* workers as it results from the following recapitulation:

	hamulus worker	*vinosus* worker	*unimaculatus* worker	Haitian gyne
HW (mm)	1.68–1.96	1.92–2.12	1.68–2.16	2.12
EL (mm)	0.44–0.52	0.54–0.56	0.48–0.55	0.56
PeW (mm)	0.72–0.86	0.84–0.88	0.64–1.00	0.76

The most visible character distinguishing *hamulus* from *vinosus* and *unimaculatus* workers, however, is the coloration of the gaster; the Haitian gyne is without gaster.

Distribution: Hispaniola.

Cephalotes auricomus (WHEELER) new status and new combination
Figs. 20, 27, 28, 29, 30, 31, 353, 354, 381

Hypocryptocerus haemorrhoidalis auricomus WHEELER, 1936 b: 202. Worker. Original description. Type locality: Sanchez (Dominican Republic). Type material: 12 syntype workers in the MCZC (KEMPF, 1951: 148), 1 syntype worker in MZSP, all examined.

Hypocryptocerus haemorrhoidalis auricomus WHEELER, KEMPF, 1951: 148. Worker.

Zacryptocerus haemorrhoidalis auricomus (WHEELER), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *hamulus* clade characterised by the following apomorphy: posterior fourth of the head dorsum, mesosoma and pedicel covered by dense, thick, golden hairs.

Worker (Figs. 27, 354). - Vertexal angles round, with crenulate margin; vertexal margin gently concave. Vertex with a trace of transversal carina and medially with a pair of small denticles more protruding in larger individuals. Eyes convex. Remaining cephalic morphology as in *hamulus* .

Mesosoma robust, convex in side view. Scapular angles rounded or with a small spine. Anterior pronotal border marked by a faint carina more impressed in smaller individuals. Humeral angles with a pair of obtuse or pointed spines directed anteriorly. Pronotal sides straight, ending posteriorly in a small tooth visible in dorsal view. Promesonotal suture variably impressed. Mesonotal teeth absent or minute and round. Propodeal suture deeply impressed dorsally. Propodeum with differentiate basal and declivous faces. Basal face more than 1/3 broader than long, with slightly convex sides anteriorly, straightening posteriorly and with or without a small denticle; declivous face as long as the basal face, with slightly converging sides posteriorly. Propodeal spines subequal in length to the basal face of the propodeum, generally thin and diverging.

Petiole ca. 1/2 broader than long, its anterior face truncate and slightly concave; its sides converging posteriorly and bearing anteriorly a small spine and medially a pointed tooth of variable size. Postpetiole broader and longer than the petiole; postpetiolar spines broad and variably pointed, inserted anteriorly and curved backwards.

Gaster and legs as in *hamulus*.

Sculpture. Head minutely reticulate; vertexal area covered by broad impressions or irregular foveae gradually shallower towards the cheeks, sparser on the anterior half of the head.

Mesosoma, petiole and postpetiole covered by strong, longitudinal, irregular striae and superficial reticulation less impressed on the pronotum. Declivous face of the propodeum completely or partially covered by thick, longitudinal striae and reticulation.

First gastral tergite reticulate without longitudinal rugosities on part or on the whole of its surface. Corresponding sternite with superficial longitudinal rugosities on the sides, the rest with impressed reticulation, opaque or faintly reticulate and slightly shining in the middle.

Coxae with sparse, transversal or longitudinal rugosities and punctate, sometimes only reticulate. Remaining parts of the legs as in *hamulus*.

Pilosity. Body with the following types of hairs: (1) truncate, erect to suberect, long on the vertexal area, on the mesosoma and on the pedicel, shorter on the anterior part of the head, on the gaster and on the legs; (2) thick, dense and appressed, long on the vertexal area, on the

Fig. 27. *Cephalotes auricomus* (WHEELER). Worker from the Dominican Republic: head in dorsal view of a specimen from Villa Altagracia (top) and meso- and metasoma in dorsal view of a specimen from Puerto Plata (bottom).

mesosoma and pedicel, shorter, thinner and sparser on the two anterior thirds of the head dorsum, on the extensor face of the femora and on the gastral tergites; (4) thin, appressed and short on the legs, on the sternites, and on the ventral sides of the first tergite; (5) thin, pointed, erect, sparse and long on the gastral sternites.

Colour. Black. Frontal carinae and scapes dark orange to light brown. Posterior fourth of the head dorsum and propodeum with golden reflexes.

Measurements (in mm) and indices: TL 5.72–7.04; HL 1.44–1.72; HW 1.52–1.96; EL 0.44–0.54; PW 1.40–1.80; PeW 0.64–0.80; PpW 0.75–0.92; HBaL 0.60–0.76; HBaW 0.16–0.21; CI 105.5–113.9; PI 106.3–114.3; PPeI 200.0–256.2; PPpI 178.7–195.6; HBaI 26.3–29.4.

G y n e (Figs. 28, 353) (previously undescribed). - Head subquadrate and convex, without disc. Frontal carinae not covering completely the cheeks. Vertexal angles subround, with crenulate margin; vertexal margin gently concave medially. Vertex with a pair of median denticles and with a trace of transversal carina in some specimens only. Ocelli far from the vertexal border. Middle of the head dorsum with a superficial depression. Clypeus concave anteriorly. Mandibles without lateral, carinate tumulus. Cheeks marginate.

Mesosoma. Scapular angles visible in dorsal view. Humeral angles with a pair of pointed anterior teeth. Pronotal sides straight. Pronotal carina strongly marked by a row of pointed denticles, shortly interrupted in the middle only. Mesonotum and scutellum flat to convex. Lower mesopleurae with a stout denticle. Basal face of propodeum converging posteriorly and with a pair of teeth; declivous face flat.

Petiole with the anterior face truncate and oblique; its sides converging posteriorly and unarmed. Postpetiole convex dorsally, with the sides convex anteriorly, converging posteriorly and unarmed.

Gaster with a broad anterior border but without true anterior lobes.

Legs as in the worker.

Wings. Fore wings with *R+Sc* superficially connected to a marked pterostigma. *2r* marked, *Rsf5* connected with *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; distal part of *M*, of *CuA* and of *1A* vestigial.

Sculpture. Vertexal area irregularly foveolate-rugulose, this sculpture is substituted anteriorly by dense, small foveae superimposed to minute reticulation. The foveae more regular and deeper on the posterior half of the frons. Ventral side of the head laterally covered by thick, regular or irregular striae and reticulate; the striae on the anterior half are substituted by foveae in some specimens. Hypostomal area deeply reticulate and with sparse, superficial foveae. Cheeks reticulate and foveolate.

Mesosoma and pedicel reticulate and covered by foveae of irregular shape, sometimes also with additional irregular rugosities. Mesopleurae with foveae more regular than on the other mesosomal parts. Metapleurae reticulate and with few, faint rugosities. Declivous face of the propodeum reticulate and with or without longitudinal rugosities. First gastral tergite and sternite reticulate and with small, superficial, piligerous punctures. Central part of the first gastral sternite moderately shining.

Pilosity as in the worker but with the appressed hairs slightly thinner and shorter.

Colour. Black. Frontal carinae and scapes dark ferrugineous. Golden reflexes less than in the worker.

Measurements (in mm) and indices: TL 9.78–10.00; HL 1.96–2.00; HW 2.04–2.16; EL 0.53–0.55; PW 2.08–2.20; PeW 0.70–0.74; PpW 0.80–0.81; HBaL 0.80; HBaW 0.23–0.24; CI 104.1–108.0; PI 98.1–98.2; PPeI 297.1–297.3; PPpI 256.8–275.0; HBaI 28.7–30.0.

M a l e (Fig. 29) (previously undescribed). - Head (eyes included, mandibles excluded) about 1/3 broader than long; vertexal margin marked as an interruption of the sculpture, straight and ending in gently convex angles. Behind the vertexal margin the head narrows in a short but visible "neck". Vertex convex. Ocelli protuberant. Eyes convex, in the middle of the sides of the head. Frontal carinae converging anteriorly, diverging backwards and not reaching the posterior border of the eyes. Frons flat, slightly concave in the middle and separate from the clypeus by a furrow. Clypeus convex, its posterior half higher than the anterior one, almost truncate. Mandibles without lateral carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

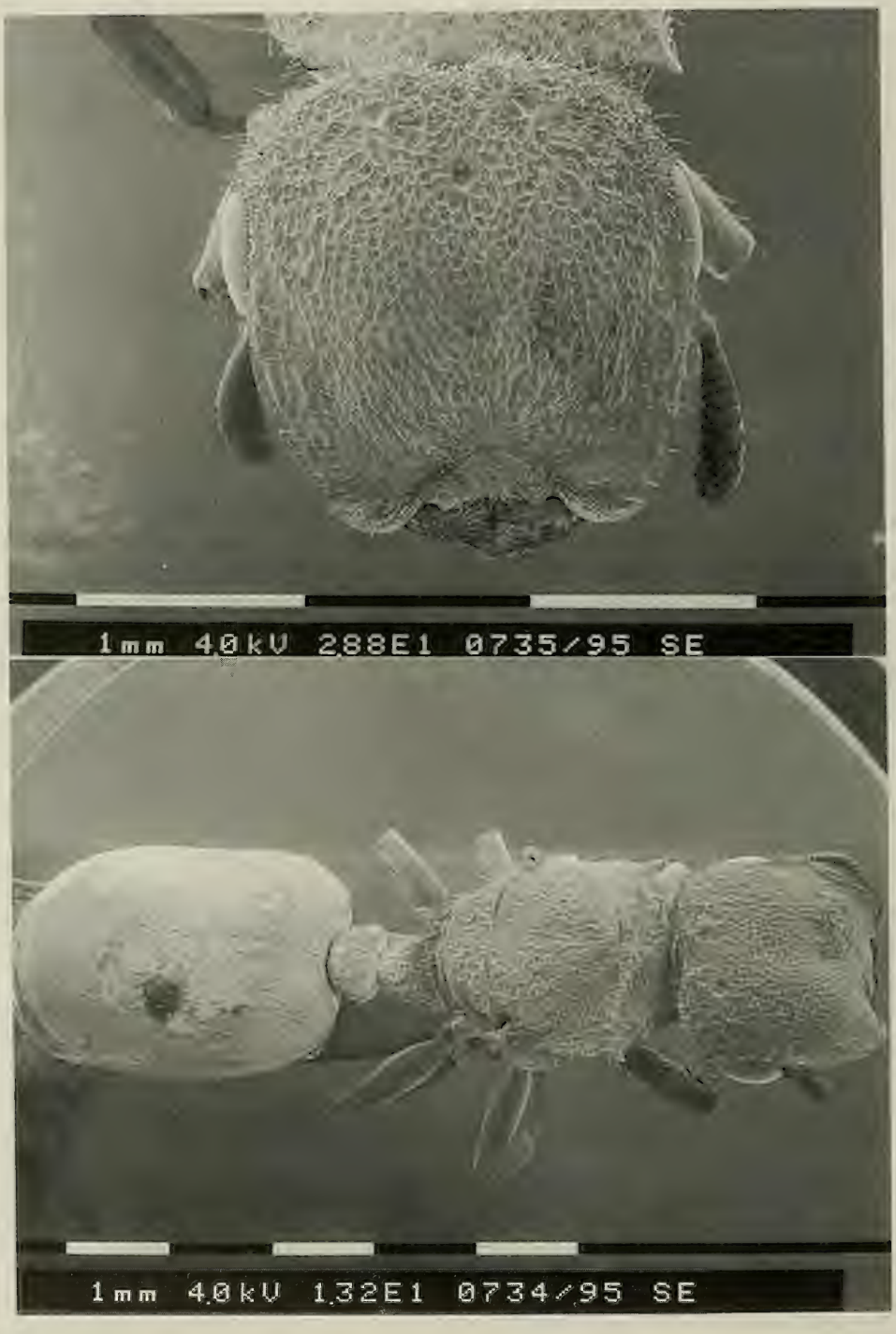


Fig. 28. *Cephalotes auricomus* (WHEELER). Gyne from Puerto Plata, Dominican Republic: head (top) and meso- and metasoma (bottom) in dorsal view.

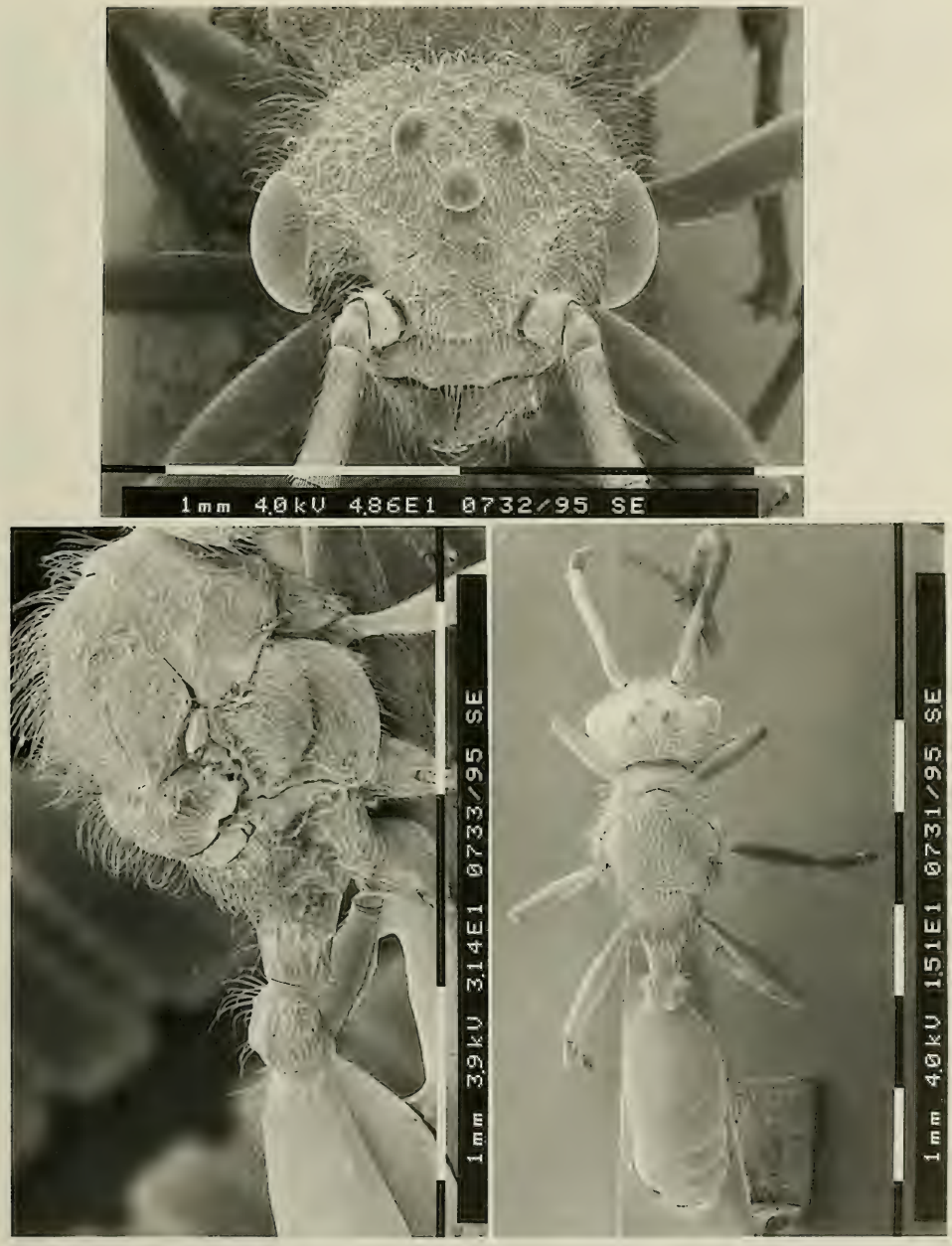


Fig. 29. *Cephalotes auricomus* (WHEELER). Male from Puerto Plata, Dominican Republic: head (top) and (bottom) mesosoma in lateral view and whole body in dorsal view.

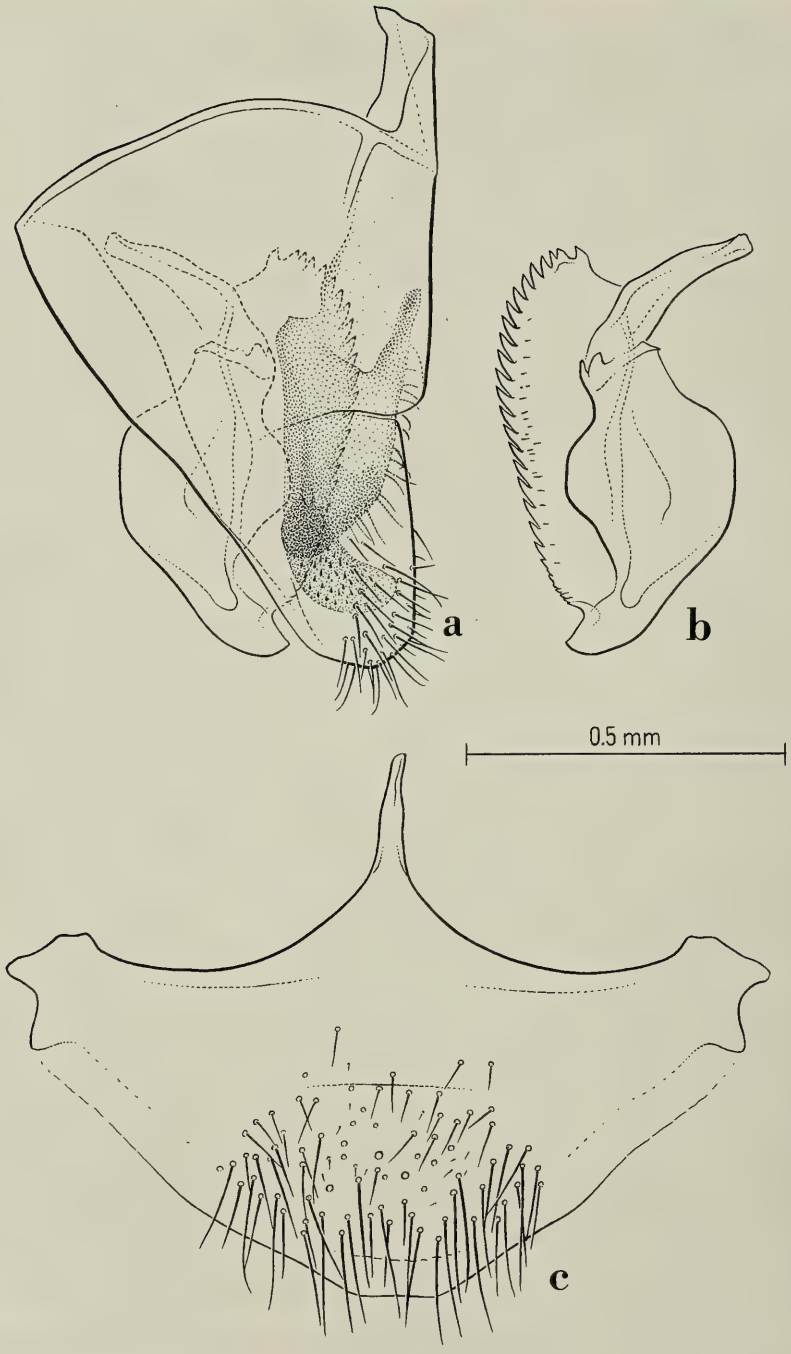


Fig. 30. *Cephalotes auricomus* (WHEELER). Male from Puerto Plata, Dominican Republic. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Mesosoma. Pronotum in dorsal view with strongly convex anterior border, broadening backwards, superficially carinate on the sides and with marked scapular angles; mesonotum convex; median Mayrian carina and parapsidal furrows weakly impressed; scutellum convex, its sides converging posteriorly; propodeum with differentiate basal and declivous faces; basal face with the sides converging posteriorly and with a pair of pointed teeth; declivous face with converging sides and laterally carinate.

Petiole narrower than the postpetiole and with the anterior border gently concave; its dorsum flat and gently sloping anteriorly; petiolar sides convex anteriorly and narrowing posteriorly. Postpetiole almost flat and with a superficial concavity dorsally; anterior third of the postpetiolar sides with a pair of short, pointed teeth.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 30.

Wings as in Fig. 31.

Sculpture. Head and mesosoma reticulate; this sculpture is superimposed by irregular, small foveae and irregular rugosities less impressed on the frons. Metapleurae, declivous face of the propodeum, petiole and postpetiole superficially reticulate and with thick striae, more regular on the pedicel, thinner and fainter on the postpetiole. First gastral tergite strongly reticulate, some specimens with thin, faint, short rugulosities on the anterior fourth. Remaining tergites and sternites superficially reticulate and shining. Legs punctate, the punctuations more impressed and denser on the tibiae.

Pilosity. Head and mesosoma covered by dense, long, suberect hairs, the same hairs sparser on the pedicel, on the gaster and equally sparse and shorter on the legs. Legs and gaster with other, similar but thinner and shorter hairs, appressed. Funiculi densely covered by thin, short, decumbent hairs.

Colour. Head, mesosoma, peduncular segments and coxae black. Mandibles and antennae, brown, first gastral segment ferrugineous. Scape, first funicular joint, masticatory margin of

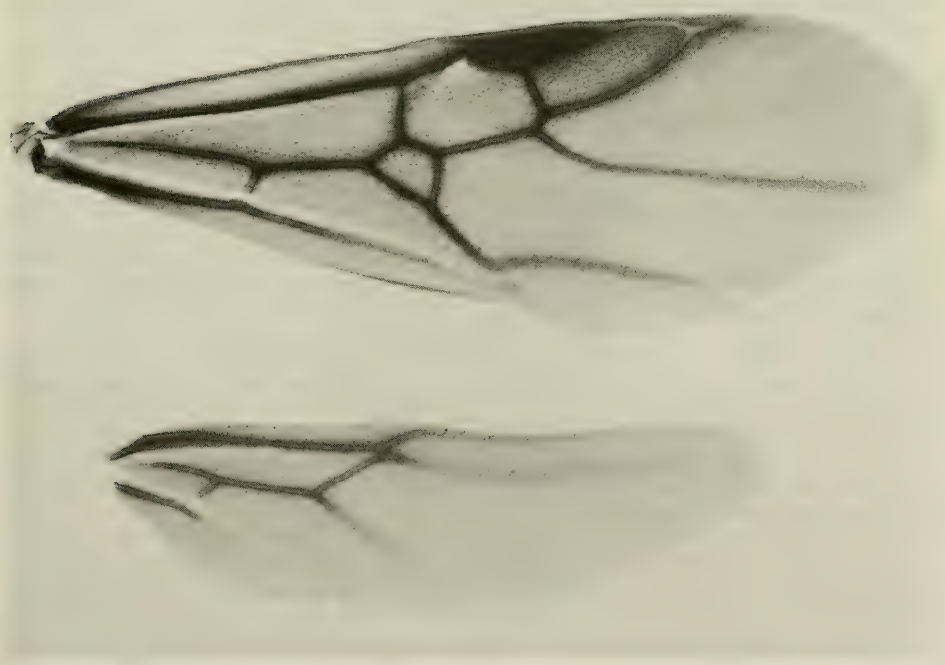


Fig. 31. *Cephalotes auricomus* (WHEELER). Male from Puerto Plata, Dominican Republic, fore and hind wings.

the mandibles, gaster and legs dark orange; proximal half of the femora and remaining funicular joints darker.

Measurements (in mm) and indices: TL 7.06–7.20; HL 1.04–1.08; HW 1.20–1.24; EL 0.50–0.52; PW 1.12–1.16; PeW 0.50–0.51; PpW 0.58–0.60; HBaL 0.87–0.89; HBaW 0.13; CI 111.1–119.2; PI 103.4–110.7; PPeI 219.6–232.0; PPpI 193.1–1293.3; HBaI 14.6–14.9.

Material examined. - **Dominican Republic**: Sanches, 22–27.V.1915, 5 workers (syntypes); Sanches, 28–31.V.1915, 6 workers (syntypes); Sanches, July, 1938, 2 workers, DARLINGTON; Villa Altagracia, July, 1938, 5 workers, DARLINGTON; Puerto Plata, 29.VIII–02.IX.1938, 2 workers, DARLINGTON [all MCZC]; Sanches, 11–16.V.1915, 1 worker (syntype) [MZSP]; San Lorenzo, 27–29.VI.1915, 1 worker (erroneously labelled as syntype) [MZSP]; Puerto Plata, km NW of Sabaneta de Yasica, 01.II.1975, 2 workers, W. L. BROWN [MCZC]; Blanton mine N of San Christobal, 26.VII.1917, 1 worker, H. MORRISON [USNM]; Carretera Luperón, km 17 from Puerto Plata, 02.VI.1995, several workers, gynes and males, M. L. DE ANDRADE [CPCC, INPA, LACM, MCSN, MCZC, MHNG, MNHN, MZSP, NHMB, SMNS, USNM, ZSMC, BMNH].

Discussion. - *C. auricomus* is easily distinguished by the pilosity covering most of the body sculpture. Its closest relative is the fossil *resinae*. Both species share - together with *hamulus* - the black body and the thick, longitudinal striae on the ventral side of the head. *Auricomus*, however, differs from *resinae* by its much thicker pilosity over the whole body, and from *hamulus*by the absence of longitudinal rugae on the anterior fourth of the first gastral tergite and by its much denser hairs.

C. auricomus also shares with *unimaculatus* and *vinosus* the ventral part of the sides of the head with thick, longitudinal striae, but *unimaculatus* and *vinosus* have different gastral coloration and less abundant pilosity. This taxon, originally described as a subspecies of *haemorrhoidalis*, in our opinion appears to be sufficiently different from its closest relatives (with which it is sympatric) as to deserve specific rank.

Distribution: Dominican Republic.

Cephalotes resinae DE ANDRADE new species

Figs. 12 B, 32

Type material: holotype worker (unique) in the copal sample Do–3566 of the SMNS.

Derivatio nominis: From the Latin "*resina*" (= resin), a name meant to contrast with fossilised resin (i. e. amber) and referred to the copal in which the sole known specimen is embedded.

Diagnosis. - A member of the *hamulus* clade characterised by the thick and regular striation, by the pilosity hiding the sculpture and by the first gastral tergite black and with long, thick hairs.

Worker (Fig. 32). - Vertexal angles round, with crenulate margin; vertexal margin gently concave medially. Vertex with a trace of transversal carina and a median pair of small denticles. Eyes convex. Other head parts as in *hamulus*.

Mesosoma robust, convex in side view. Scapular angles well visible. Anterior pronotal border marked by an impressed carina. Humeral angles with a pair of spines directed antero-laterally and with round tips. Pronotal sides straight, ending in a small, round tooth visible in dorsal view. Promesonotal suture impressed on the sides. Mesonotal teeth absent. Propodeal suture deeply impressed. Propodeum with differentiate basal and declivous faces. Basal face of the propodeum ca. 1/3 broader than long and with straight sides; declivous face with posteriorly slightly converging sides. Propodeal spine (only the left one intact) shorter than the basal face of the propodeum, thin and oriented postero-laterally.

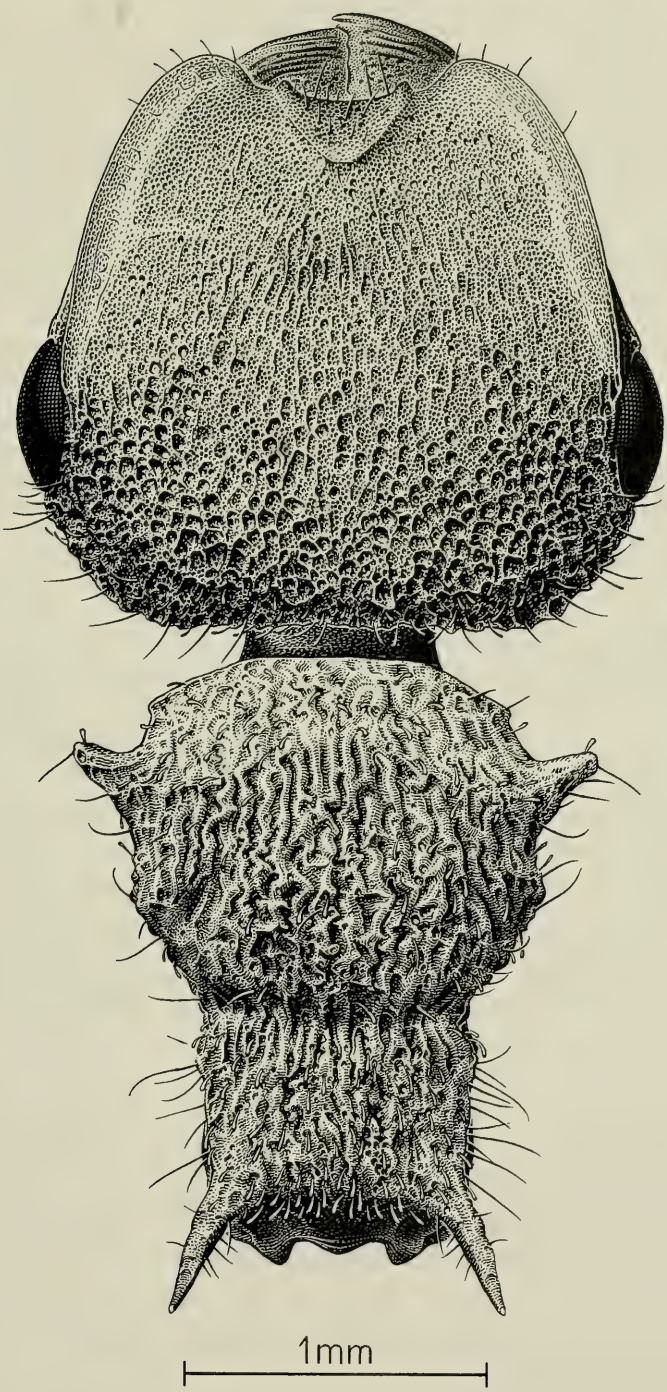


Fig. 32. *Cephalotes resinae* DE ANDRADE. Worker from Dominican copal. Dorsal view of head and mesosoma.

Petiole ca. 1/2 broader than long, its anterior face truncate and marginate dorsally by a crenulate carina interrupt in the middle; its sides converging posteriorly, with a pointed medial tooth 1/2 of the length of the petiole. Postpetiole ca. 2/3 broader than long, and as long as the petiole; postpetiolar spines pointed, inserted anteriorly and curved backwards.

Gaster with a narrow, lamellaceous anterior border reaching the first gastral stigma.

Legs as in *hamulus*.

Sculpture. Head minutely reticulate; vertexal area covered by broad impressions or irregular foveae gradually shallower towards the cheeks. Anterior part of the head with small, superficial, sparse foveae. Frontal carinae coarsely reticulate. Ventral side of the head laterally covered by strong longitudinal striae. Cheeks punctate and superficially rugulose.

Mesosoma, petiole and postpetiole covered by strong, longitudinal, irregular striae, and superficial reticulation. Declivous face of the propodeum with thick, curved striae and deep reticulation.

First gastral tergite covered by reticulation and faint, small, very superficial foveae; its anterior fourth with longitudinal rugosities close to the articulation with the petiole. Corresponding sternite with superficial, longitudinal, lateral rugosities on the anterior half, the rest with impressed reticulation, and rare piligerous foveae smaller than those on the first tergite.

Legs as in *hamulus*.

Pilosity. Body with the following types of hairs: (1) truncate, erect to suberect, long on the vertexal area, on the mesosoma and on the pedicel, shorter on the anterior part of the head, on the gastral tergites and on the legs; (2) thick, sparse and appressed, long on the vertexal area, on the mesosoma and pedicel, slightly shorter and thinner on the anterior half of the head and on the gastral tergites; (3) thin, rare, appressed and short on the legs; (4) thin, pointed, erect, sparse and long on the gastral sternites.

Colour. Black. Frontal carinae lighter.

Measurements (in mm) and indices: TL 6.84; HL 1.72; HW 1.92; EL 0.52; PW 1.72; PeW 0.80; PpW 1.00; HBaL 0.64; HBaW 0.19; CI 111.6; PI 111.6; PPeI 215.0; PPpI 172.0; HBaI 29.7.

Material examined. - **Dominican Republic**: A single worker (holotype) embedded in copal without exact locality [SMNS, No. Do–3566].

Discussion. - *C. resinae* appears to be the sister species of the Recent *auricomus*, also known from the Dominican Republic only. Both species share the dense body striation, the black colour and the first gastral tergite with thick, long hairs.

It is noteworthy that both copal species described from the Dominican Republic in this paper (*taino* and *resinae*) but none of the much more numerous true fossils from Dominican amber belong to the Recent Hispaniolan endemic *hamulus* clade.

Distribution: Dominican Republic (copal).

Cephalotes vinosus (WHEELER) new status, new combination

Hypocryptocerus haemorrhoidalis vinosus WHEELER, 1936 b: 202. Worker. Original description. Type locality: Mt. Rochelois (Haiti). Type material: 22 syntype workers in MCZC, 3 syntype workers in MZSP (examined).

Zacryptocerus haemorrhoidalis vinosus (WHEELER), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *hamulus* clade characterised by the first gastral tergite reddish-brown.

Worker. - Vertexal angles round, with crenulate margin; vertexal margin gently concave medially. Vertex with a median pair of small denticles and – in larger individuals only – a trace of transversal carina. Eyes slightly convex. The rest as in *hamulus*.

Mesosoma robust, convex in side view. Scapular angles bearing a small denticle. Anterior pronotal border marked by a carina. Humeral angles with a pair of obtuse or round spines directed anteriorly. Pronotal sides straight, ending in a small tooth visible in dorsal view. Mesonotal teeth small and rounded. Propodeal suture deeply impressed. Propodeum with differentiate basal and declivous faces. Basal face slightly more than 1/3 broader than long, with sides convex anteriorly straightening posteriorly and with or without 1–2 small denticles; declivous face as long as the basal face, with posteriorly slightly converging sides. Propodeal spines shorter than the basal face of the propodeum, thick in most specimens and diverging.

Petiole ca. 1/2 broader than long, its anterior face truncate and gently concave; its sides converging posteriorly and bearing a pair of median pointed teeth. Postpetiole broader than and as long as the petiole; postpetiolar spines broad and variably pointed, inserted anteriorly and curved backwards.

Gaster with a lamellaceous anterior border, generally broad, sometimes reduced, reaching the first gastral stigma at maximum.

Legs as in *hamulus*.

Sculpture. Head minutely reticulate; vertexal area covered by broad impressions or foveae gradually shallower towards the cheeks. Anterior half of the head with small and shallow foveae. Frontal carinae reticulate and faintly rugulose. Ventral side of the head laterally covered by thick regular striae and reticulate. Hypostomal area deeply reticulate. Cheeks reticulate and superficially rugulose on their posterior half.

Mesosoma, petiole and postpetiole covered by thick, longitudinal, irregular striae and superficial reticulation less impressed on the pronotum. Declivous face of the propodeum covered by thick, longitudinal striae and reticulate.

First gastral tergite reticulate and with longitudinal rugosities on its anterior fourth. Corresponding sternite with superficial longitudinal rugosities on the sides, ventrally with impressed reticulation and opaque, or faintly reticulate and slightly shining in the middle, with sparse piligerous fossae.

Legs as in *hamulus*.

Pilosity. As in *hamulus* but denser.

Colour. Head, mesosoma, peduncular segments, gastral sternites, lateral border of first tergite, remaining tergites, and legs black. Frontal carinae, scapes, dark orange to light brown. Gastral dorsum dark reddish. Vertexal area, mesosoma and pedicel with some golden reflexes.

Measurements (in mm) and indices: TL 6.84–7.56; HL 1.76–1.92; HW 1.92–2.12; EL 0.54–0.56; PW 1.76–1.92; PeW 0.84–0.88; PpW 1.04–1.16; HBaL 0.72–0.76; HBaW 0.20–0.21; CI 109.1–113.3; PI 108.5–110.4; PPeI 209.5–223.8; PPpI 164.3–174.0; HBaI 26.3–27.7.

Material examined. - **Haiti**: Mt. Rochelois, 25 workers (syntypes), W. J. EYERDAM, "very pugnacious, habitat: nest in a beech" [MCZC, MZSP].

Discussion. - *C. vinosus*, known on the type series only, is characterised by the dark red gastral dorsum. Its sister species is *unimaculatus*. Both share the dense body striation, the longitudinal rugae on the anterior part of the first gastral tergite and the pilosity not hiding the sculpture. Some specimens of *hamulus* also exhibit a gastral dorsum with reddish areas as in *vinosus*. The petiole and postpetiole of *vinosus*, however, are much broader than those of *hamulus* as shown by the relative values of PeW and PpW. The postpetiolar spines of *vinosus*, in addition, are also much broader than those of *hamulus*. Since these two characters (peduncular morphology and size) appear to be constantly different in all the specimens of *vinosus* and *hamulus* (25 and 26 respectively) available for the present study, we regard these two taxa as separate species. *Vinosus*, in addition, can be separated from its sister species *unimaculatus* for the coloration of the gaster, completely red, instead of yellow with a black spot. According to the material available for the present study the two species differ also in the relative values of the PPpI.

Distribution: Haiti.

Cephalotes unimaculatus (SMITH) bona species and new combination

Figs. 33, 34

Cryptocerus unimaculatus SMITH, 1854: 221, pl. 19 fig. 9. Worker. Original description. Type locality: Brazil (certainly erroneous). Type material: holotype worker labelled "Braz., *Cryptocerus unimaculatus* Smith." in the BMNH (KEMPF, 1951: 151), examined.

Cryptocerus hamulus steinheili FOREL, 1908 a: 355. Worker. Original description. Type locality: Antille St. Thomas (probably erroneous). Type material: three syntype workers labelled "St. Thom. cotypus" in MHNG (examined). Synonymy by KEMPF, 1951: 151.

Hypocryptocerus haemorrhoidalis unimaculatus (SMITH), KEMPF, 1951: 151. Worker. First combination in *Hypocryptocerus*.

Hypocryptocerus haemorrhoidalis signatus WHEELER, 1936 b: 203. Worker. Original description. Type locality: Mont Basil (Haiti). Type material: holotype worker (unique) in the MCZC (examined). New synonym.

Hypocryptocerus haemorrhoidalis signatus WHEELER, KEMPF, 1951: 150. Worker.

Fig. 33. *Cephalotes unimaculatus* (SMITH). Worker from Bani, Dominican Republic, general habitus.

Zacryptocerus haemorrhoidalis signatus (WHEELER), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

Zacryptocerus haemorrhoidalis unimaculatus (SMITH), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *hamulus* clade characterised by the following apomorphy: first gastral tergite yellowish-orange with an oval or triangular, postero-medial black spot.

W o r k e r (Fig. 33). - Head shape as in the other species of the group. Eyes flat or convex.

Mesosoma robust, convex in side view. Scapular angles bearing a small denticle. Anterior pronotal border marked by a carina more impressed in larger individuals. Humeral angles with a pair of obtuse spines directed anteriorly. Pronotal sides straight, ending in a small tooth visible in dorsal view. Promesonotal suture variably impressed. Mesonotal teeth absent. Propodeal suture deeply impressed. Propodeum with differentiated basal and declivous faces. Basal face ca. 1/3 broader than long, with slightly convex sides anteriorly. Straightening posteriorly and with or without a small denticle; declivous face as long as the basal face, with slightly converging sides posteriorly, without central concavity. Propodeal spines as long as or longer than the basal face of the propodeum, thick in most specimens, diverging.

Petiole ca. 1/3 broader than long, its anterior face truncate and marginate dorsally by a crenulate carina interrupted in the middle; its sides converging posteriorly and with a pointed tooth medially, sometimes reduced to a minute denticles in some specimens. Postpetiole as broad as or broader and longer than the petiole; postpetiolar spines broad and variably pointed, inserted anteriorly and curved backwards.

Gaster and legs as in *hamulus*.

Sculpture. Head minutely reticulate; vertexal area covered by broad impressions or foveae gradually shallower towards the cheeks. Anterior half of the head with small and faint foveae. Head dorsum between the frontal carinae covered by coarse reticulation superimposed by shallower foveae and faint, thin longitudinal rugosities. Frontal carinae coarsely reticulate. Ventral side of the head laterally covered by strong longitudinal striae. Cheeks punctated and superficially rugulose.

Mesosoma, petiole and postpetiole covered by strong, longitudinal, irregular striae, and superficial reticulation. Declivous face of the propodeum covered by thick, longitudinal, transversal or curve striae and reticulation superficial to deep. Anterior petiolar face covered by thick, longitudinal or transversal striae; some specimens have longitudinal higher striae substituted by transversal striation on the lower part.

First gastral tergite reticulate with or without superficial, longitudinal rugosities on part or on the whole of its surface. Corresponding sternite with superficial longitudinal rugosities on its sides, the rest with impressed reticulation and opaque or faintly reticulated and slightly shining.

Legs as in the other species of the group. Some specimens with transversal rugosities on the anterior and posterior faces of the femora.

Pilosity. As in *hamulus*.

Colour. Head, mesosoma, pedicel, sternites, ventral marginal area of first tergite and remaining tergites black, legs lighter. Frontal carinae, scapes, first funicular joints, tips of pronotal and propodeal spines dark orange to light brown; last funicular joints brown. Gastral dorsum and its ventro-external parts orange with a black, oval stripe from the posterior half up to the end of the first tergite. The black spot, anteriorly, can be rounded, broadly or narrowly triangular, or gently concave in different specimens.

Measurements (in mm) and indices: TL 5.6–7.8; HL 1.40–1.80; HW 1.68–2.16; EL 0.48–0.55; PW 1.60–2.00; PeW 0.64–1.00; PpW 0.88–1.08; HBaL 0.62–0.76; HBaW 0.16–0.22; CI 109.1–120.0; PI 102.1–112.2; PPeI 188.0–256.2; PPpI 173.9–192.3; HBaI 25.8–28.9.

M a l e (previously undescribed). - Head (eyes included, mandibles excluded) about 1/3 broader than long. Vertexal margin incompletely carinate and straight. Vertexal angles obtuse, diverging towards the posterior border of the eyes. Vertex convex. Ocelli protuberant. Eyes

convex. Frontal carinae converging anteriorly, diverging backwards and not reaching the posterior border of the eyes. Clypeus convex, its posterior half higher than the anterior one, almost truncate. Anterior border of the clypeus bidentate, concave medially and laterally. Mandibles without lateral carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with convex anterior border. Scapular angles well visible in dorsal view. Humeral angles with a pair of pointed denticles. Pronotal sides marginate. Pronotal carina marked. Mesonotum convex; median Mayrian carina weakly impressed. Propodeum with differentiate basal and declivous faces; basal face with the sides gently converging posteriorly and with a pair of broad, pointed teeth; declivous face with converging sides and superficially carinate laterally.

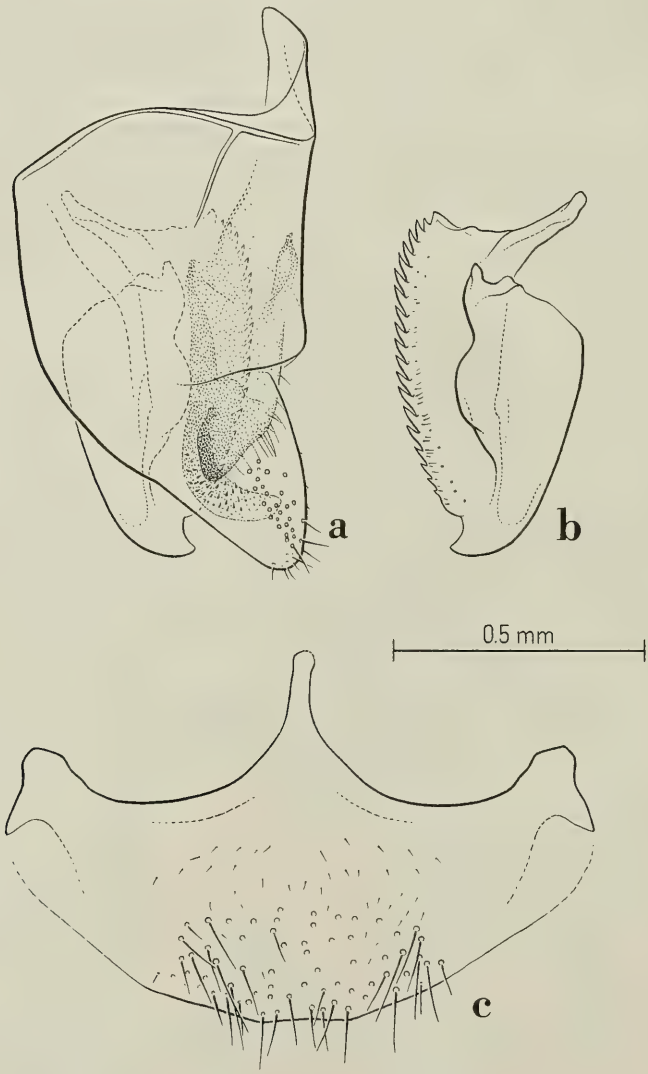


Fig. 34. *Cephalotes unimaculatus* (SMITH). Male from San José de las Matas, Dominican Republic. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Petiole narrower than the postpetiole and with the anterior border superficially concave; its dorsum flat, gently sloping anteriorly and marginate laterally; petiolar sides convex anteriorly and narrowing posteriorly. Postpetiole almost flat dorsally; posterior part of the dorsum with a pair of minute denticles. Anterior third of the sides of the postpetiole with a pair of short, pointed teeth.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 34.

Wings as in *auricomus*.

Sculpture. Head and mesosoma with minute reticulation; this sculpture is superimposed by irregular foveae and irregular rugosities, the rugosities transversal around the eyes, longitudinal on the frons and on the scutellum and absent on the mesonotum; the foveae more regular on the mesonotum. Declivous face of the propodeum and pleurae superficially reticulate, shining and with longitudinal, thick rugosities on the pro- and mesopleurae, irregular on the declivous face of the propodeum and on the metapleurae. Petiole and postpetiole reticulate and with irregular, longitudinal rugosities, more concentric on the dorsum of the postpetiole. First gastral tergite strongly reticulate. Remaining tergites and sternites superficially reticulate. Legs punctate, the punctures more impressed and denser on the tibiae.

Pilosity. As in *hamulus*.

Colour. Head, mesosoma and petiole black. Coxae and postpetiole brown. Gaster and legs orange.

Measurements (in mm) and indices: TL 6.64–7.20; HL 0.96–1.14; HW 1.14–1.32; EL 0.51–0.55; PW 1.08–1.28; PeW 0.44–0.51; PpW 0.52–0.54; HBaL 0.88–0.92; HBaW 0.12–0.14; CI 115.8–118.7; PI 103.1–105.5; PPeI 245.4–251.0; PPpI 207.7–237.0; HBaI 13.6–15.2.

Note: the male measurement are based on the sole two specimens available, an adult and a pupa. This fact should account for the differences between them. The lowest figures, however, refer always to the pupa.

Material examined: Holotype worker with certainly erroneous locality label (Brazil) (BMNH).

?**St. Thomas** (doubtful record), 3 workers (syntypes of *steinheili* Forel) [MHNG].

Dominican Republic: no further locality, intercepted in POE San Juan, Puerto Rico, in wood (trunk), 07.I.1980, 7 workers, 1 male (pupa), G. Greene [USNM]; Prov. Pedernales, 10 and 14 km N of Cabo Rojo, 30–45 m, 150 m, 19.VIII.1988, thorn scrub-trop. dry forest, 5 workers, M. A. Ivie, T. K. Philips & K. A. Johnson [USNM]; Prov. Pedernales, 30 km N of Cabo Rojo, 140 m, 19.VIII.1988, pine forest, 1 worker [USNM]; Prov. Pedernales, 13.5 km N of Cabo Rojo, 140 m, 21.VIII.1988, cactus-thorn scrub, beating, 1 worker [USNM]; Prov. Pedernales, 25 km N of Cabo Rojo, 09.X.1988, wet forest at light & night beating, 1 worker, M. A. Ivie, T. K. Philips & K. A. Johnson [USNM]; San José de las Matas, 1,000–2,000 ft., June 1938, 1 male, Darlington [MCZC]; Bani, 65 m, 20.II.1971, 21.III.1971, 31.III.1971, 11.IV.1971, 25 workers, J. & S. Klapperich [CPCC, NHMB, MZSP, MCZC].

Haiti: Mt. Basil, Summit 4500', 09.IX.1934, 1 worker (holotype of *signatus*), J. P. Darlington [MCZC].

Discussion. - *C. unimaculatus* has been described from Brazil, a provenance confirmed by the label of the holotype which must nonetheless be considered as certainly wrong. This species is remarkable for its coloration. Kempf (1951) separated *unimaculatus* from *signatus* (an imperfectly known infraspecific taxon described on a unique worker) on the base of the colour and sculpture but he doubted the utility of this separation. Actually, the material available for the present study confirmed the poor discriminatory value of the chromatic differences distinguishing *signatus* from *unimaculatus* in most specimens available to us. The synonymy between the two, hence, appears unavoidable.

The closest relative of *unimaculatus* is *vinosus*. Both share the regular body sculpture, the gaster differing in colour from the rest of the body and the pilosity partially hiding the sculpture.

Distribution: Hispaniola (and St. Thomas?).

Cephalotes argentiventris DE ANDRADE new species
Fig. 35

Type material: holotype worker (unique) without fore left tibia and tarsus, from Constanza, 3–4,000 ft, Dominican Republic, P. J. Darlington (MCZC).

Derivatio nominis: From the Latin *argentum* (= silver) and *venter* (= abdomen), referred to the distinctive coloration of this species.

Diagnosis. - A member of the *hamulus* clade characterised by the following two apomorphies: first gastral tergite completely covered by thick silver-yellowish hairs, and rare hairs on the remaining parts of the body.

Worker (Fig. 35). - Vertexal angles round, barely crested laterally; vertexal border concave, with a faint margin. Vertex without trace of transversal carina, with a median pair of small denticles. Cheeks marginate posteriorly. Anterior clypeal border concave in the middle and bearing two small lateral teeth. Eyes convex. Mandibles without lateral carinae and robust; masticatory margin with an developed apical tooth, a smaller preapical one and an edentate margin.

Mesosoma robust, convex in side view. Scapular angles bearing a small denticle. Anterior pronotal border marked by an impressed carina. Humeral angles with a pair of stout, obtuse spines and pointed anteriorly. Pronotal sides straight, ending in a small, round tooth visible in dorsal view. Promesonotal suture impressed. Mesonotal teeth broadly rounded. Propodeal suture deeply impressed dorsally. Propodeum ca. 1/4 narrower than the mesonotum, with differentiate basal and declivous faces. Basal face ca. 1/3 broader than long, with slightly convex sides anteriorly, straightening posteriorly and without denticles; declivous face as long as the basal face, its sides slightly converging posteriorly. Propodeal spines slightly shorter than the basal face of the propodeum, thick and diverging.

Petiole ca. 1/2 broader than long, its anterior face truncated and marginate dorsally by a crenulate carina interrupted in the middle; its sides converging posteriorly and bearing a pointed tooth medially. Postpetiole ca. 1/4 broader than and as long as the petiole; postpetiolar spines pointed, inserted anteriorly and curved backwards.

Gaster with a narrow lamellaceous anterior border, reaching the first gastral stigma at maximum.

Legs. Fore coxae without a broad lobe or angle anteriorly. Hind femora slightly inflated in the middle; mid and hind basitarsi laterally compressed in dorsal view; their sides narrowing distally in side view.

Sculpture. Head minutely reticulate; vertexal area covered by broad, irregular foveae gradually shallower towards the eyes. Frontal carinae reticulate and superficially rugulose on their sides. Ventral side of the head laterally covered by thick, sinuous striae. Hypostomal area deeply reticulate. Cheeks reticulate and superficially rugulose.

Mesosoma, petiole and postpetiole superficially covered by reticulation and longitudinal sinuous striae. Declivous face of the propodeum with thin, longitudinal striae and reticulate.

First gastral tergite covered by faint punctures. Corresponding sternite with superficial longitudinal rugosities on the anterior half of its sides, the rest with impressed reticulation and slightly shining posteriorly .

Coxae reticulate and transversally rugulose on the outer face. Femora deeply reticulate and with superficial, thin, irregular rugae on the distal part. Outer face of tibiae and basitarsi with longitudinal, anastomosing rugosities, the other faces reticulate.

Pilosity. Body with the following types of hairs: (1) truncate, erect to suberect, sparse and long on most of the body; (2) thin, sparse, appressed and short on the head, on the mesosoma and pedicel; (3) thick, dense and appressed on the gaster, sparser on the extensor face of the femora; (4) thin, pointed, erect, sparse and long on the gastral sternites.

Colour. Black. Frontal carinae, scape, first funicular joint, masticatory margin of the mandibles, tips of the pronotal, propodeal, and pedicellar spines and tarsomeres dark orange to light brown; remaining funicular joints brown. Gaster black with a silverish aspect due to the pilosity.

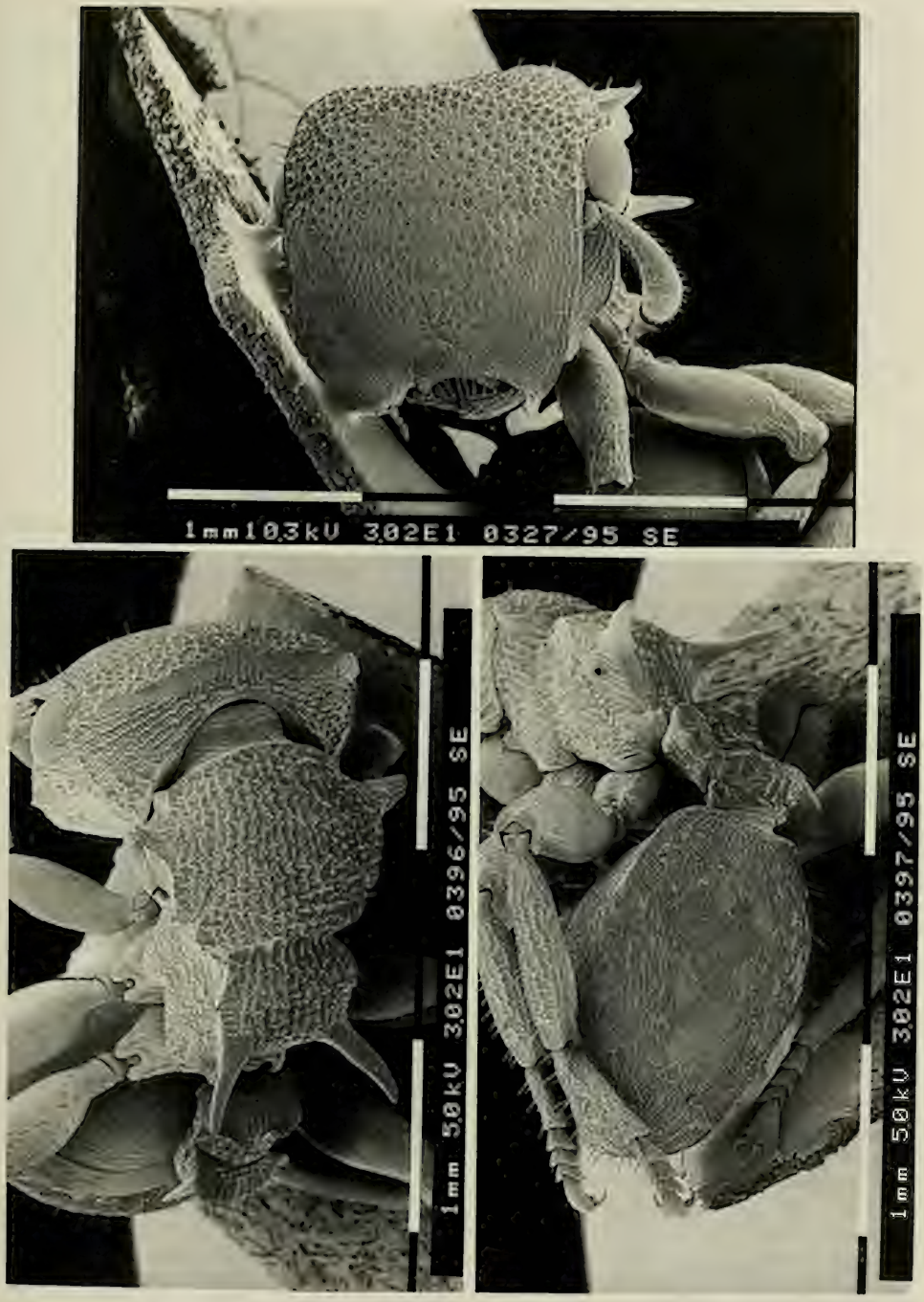


Fig. 35. *Cephalotes argentiventris* DE ANDRADE. Worker from Constanza, Dominican Republic: head in dorsal view (top) and meso- and metasoma in semi-dorsal view (bottom).

Measurements (in mm) and indices: TL 6.28; HL 1.56; HW 1.72; EL 0.48; PW 1.64; PeW 0.68; PpW 0.87; HBaL 0.64; HBaW 0.18; CI 110.2; PI 104.8; PPeI 241.1; PPpI 188.5; HBaI 28.1.

Material examined. - **Dominican Republic**: Constanza, 3–4,000 ft., August 1938, 1 worker (holotype), P. J. DARLINGTON [MCZC].

Discussion. - *C. argentiventris* is an easily distinguished species by its gastral pilosity incomparable with the other known species of the clade. *C. argentiventris* shares with *taino* and *flavigaster* the sinuous body striation and the propodeal dorsum narrower than the mesonotum; with *flavigaster* the hairs long but not hiding the sculpture. *C. argentiventris* also shares with *hamulus* and *resinae* the thick hairs on the first gastral sternite, but in *argentiventris* the hairs hide completely the gastral microsculpture.

Distribution: Dominican Republic.

Cephalotes taino DE ANDRADE new species

Fig. 36

Type material: holotype worker (unique) in the Dominican copal sample Do–3014 in the SMNS.

Derivatio nominis: From "Taino", the name of the inhabitants of the island of Hispaniola at the time of the European arrival in the Caribic.

Diagnosis. - A member of the *hamulus* clade characterised by the following combination of characters: body striation sinuous and first gastral tergite entirely reddish brown.

Worker (Fig. 36). - Vertexal angles round, with crenulate margin; vertexal margin gently concave medially. Vertex with a trace of transverse carina. Anterior clypeal border concave in the middle and bearing two small lateral teeth. Eyes convex. Mandibles without lateral carinae, robust and directed ventrally.

Mesosoma robust, convex in side view. Scapular angles bearing a small, rounded denticle. Anterior pronotal border marked by an impressed carina. Humeral angles with a pair of stout spines with subround tips, directed anterolaterally. Pronotal sides straight, ending in a rounded tooth visible in dorsal view. Promesonotal suture laterally impressed. Mesonotal teeth minute. Propodeal suture deeply impressed dorsally. Propodeum with differentiate basal and declivous faces, ca. 1/4 narrower than the mesonotum. Basal face of propodeum ca. 1/3 broader than long, with subparallel sides anteriorly and with a pair of small anterior denticles; declivous face as long as the basal one, with posteriorly slightly converging sides. Propodeal spines shorter than the basal face of the propodeum, thin and diverging.

Petiole ca. 1/3 broader than long, its anterior face truncated and marginate dorsally by a crenulate carina interrupted in the middle; its sides gently converging posteriorly in a pair of small pointed teeth medially. Postpetiole ca. 1/2 broader than and as long as the petiole; postpetiolar spines pointed, inserted anteriorly and curved backwards.

Gaster and legs as in the other species of the group.

Sculpture. Head minutely reticulate; vertexal area covered by broad impressions or foveae gradually shallower towards the eyes, sparser to rare on the anterior part of the head dorsum. Frontal carinae superficially reticulate and faintly rugulose. Ventral side of the head laterally covered by thick, sinuous striae. Hypostomal area deeply reticulate. Cheeks reticulate and superficially rugulose.

Mesosoma, petiole and postpetiole covered by superficial reticulation and irregular, thick striae ordered longitudinally on the middle of the mesosoma. Declivous face of the propodeum with few longitudinal striae .

First gastral tergite superficially reticulate and with faint, minute, superficial foveae. Corresponding sternite with superficial longitudinal rugosities on the anterior half of the si-

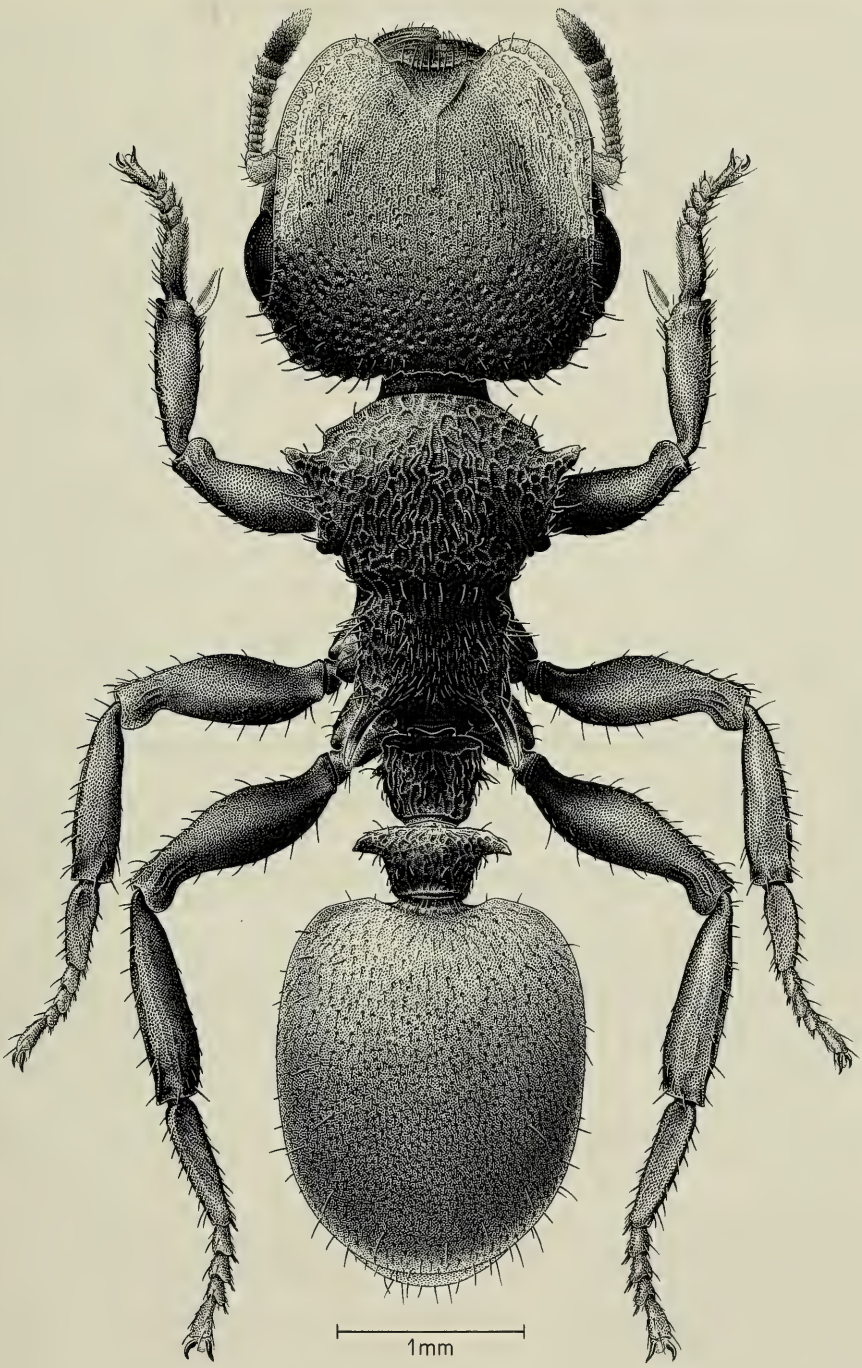


Fig. 36. *Cephalotes taino* DE ANDRADE Worker from Dominican copal. Dorsal view.

des, the rest with impressed reticulation and rare foveae smaller than those on the first gastral tergite.

Legs as in *argentiventris* but with the rugosities on the distal part of the femora more regular.

Pilosity. Body with the following types of hairs: (1) truncate, erect to suberect, of variable size on the whole body; (2) appressed, long, sparse on the vertexal area, on the pronotum, on the mesonotum and on the pedicel, slightly denser on the propodeum and on the first gastral tergite, rare on the legs; (3) thin, long and pointed on the gastral sternites.

Colour. Black. Frontal carinae, scapes, tips of the propodeal spines, and tarsomeres dark orange to light brown. Gaster reddish-brown

Measurements (in mm) and indices: TL 6.48; HL 1.64; HW 1.80; EL 0.44; PW 1.56; PeW 0.64; PpW 0.84; HBaL 0.68; HBaW 0.17; CI 109.7; PI 115.4; PPeI 243.7; PPpI 185.7; HBaI 25.0.

Material examined. - **Dominican Republic**: A worker (holotype) in copal without further locality data [SMNS, No. Do–3014].

Discussion. - *C. taino* shows clear relationships with the Recent species *flavigaster* and *argentiventris*. The three species share the sinuous body sculpture, the absence of rugosities on the anterior fourth of the gastral dorsum and the basal face of the propodeum narrow. In particular, *C. taino* shares with *flavigaster* and *vinosus* the first gastral tergite contrasting in colour with the other body parts, but *vinosus* differs from *taino* for its much denser pilosity and more regular striae. The most remarkable character of *taino* is the presence of relatively deep piligerous foveae on the gastral dorsum. Such foveae are less impressed in both *flavigaster* and *argentiventris*. We regard the copal species *taino* as possibly intermediate between the Recent species *flavigaster* and *argentiventris*. This interpretation is compatible with the position that *taino* assumes in our cladogram.

C. taino shares also with the other copal species, *resinae*, the pilosity hiding the sculpture on the basal face of the propodeum, but *resinae* differs from *taino* by its more regular striation and by its completely black body. Considering the young age of Dominican copal as given by SCHLEE (1984), i. e. less than 280 years, this species may still be discovered on the island of Hispaniola today.

It is noteworthy that both copal species described here from the Dominican Republic (*taino* and *resinae*) but none of the much more numerous true fossils from Dominican amber belong to the Recent Hispaniolan endemic *hamulus* clade.

Distribution: Dominican Republic (copal).

Cephalotes flavigaster DE ANDRADE new species

Fig. 37

Type material: holotype worker from the Dominican Republic, Constanza, 3–4,000 ft, August, 1938 (Darlington) (MCZC). Paratypes: another worker, same data as the holotype; a worker, Dominican Republic, Constanza to Jarabacoa, 2–4,000 ft, August 1938, Darlington (both MCZC).

Derivatio nominis: from the Latin *flavus* (= reddish-yellow) and *gaster* (= abdomen), referred to the distinctive coloration of this species.

Diagnosis. - A member of the *hamulus* clade characterised by a completely orange first gastral tergite and by sparse pilosity.

Worker (Fig. 37). - Vertexal angles round, with crenulate margin; vertexal margin

concave medially. Vertex with a trace of transversal carina and a median pair of small denticles. Cheeks marginate. Eyes convex.

Mesosoma robust, convex in side view. Scapular angles bearing a small denticle, more developed in the paratypes than in the holotype. Pronotal border anteriorly marked by a carina more impressed in the holotype than in the remaining specimens, slightly smaller. Humeral angles bearing each an obtuse spine directed anteriorly. Pronotal sides straight, ending posteriorly in a small, round tooth visible in dorsal view. Promesonotal suture impressed. Mesonotal teeth either rounded and poorly developed (holotype), or absent, or small and pointed. Propodeal suture deeply impressed dorsally. Propodeum ca. 1/4 narrower than mesonotum, with differentiate basal and declivous faces. Basal face slightly more than 1/3 broader than long, with a small denticle anteriorly, straightening posteriorly; declivous face as long as the basal face, with slightly converging sides posteriorly. Propodeal spines as long as (holotype) or slightly shorter than the basal face of the propodeum, thick in most specimens, diverging.

Petiole more than 1/3 broader than long, its anterior face truncated and marginate dorsally by a crenulate carina shortly interrupted in the middle; its sides converging posteriorly and bearing a small spine anteriorly, absent in one paratype, and a pointed tooth medially. Postpetiole more than 1/2 broader than longer; postpetiolar spines broad and rounded (holotype) or pointed (paratypes), inserted anteriorly and curved backwards.

Gaster with a lamellaceous narrow anterior border reaching the first gastral stigma at maximum.

Legs as in *argentiventris*.

Sculpture. Head minutely and deeply reticulate; vertexal area covered by broad, irregular foveae gradually shallower towards the eyes. Anterior part of the head with small and superficial foveae. Frontal carinae faintly rugulose. Ventral side of the head laterally covered by thick, sinuous striae. Hypostomal area deeply reticulate. Cheeks reticulate and superficially rugulose.

Mesosoma, petiole and postpetiole covered by longitudinal sinuous striae and superficial reticulation. Declivous face of the propodeum with irregular longitudinal striae and reticulate.

First gastral tergite reticulate and with superficial, sparse, small, piligerous foveae. Corresponding sternite with superficial longitudinal rugosities and impressed reticulation on the sides, ventrally with superficial reticulation and slightly shining.

Legs as in *argentiventris*.

Pilosity. As in *argentiventris* except for the first gastral tergite which bears thin, sparse hairs.

Colour. Black. Frontal carinae, tips of the pronotal, propodeal and peduncular spines, and last tarsomeres dark orange to light brown; remaining funicular joints brown. First gastral tergite opaque orange, the rest black.

Measurements (in mm) and indices: TL 6.20–7.20; HL 1.56.–1.72; HW 1.76–1.92; EL 0.48–0.52; PW 1.60–1.84; PeW 0.64–0.75; PpW 0.85–0.90; HBaL 0.64 –0.70; HBaW 0.18–0.20; CI 111.6–112.8; PI 104.3–110.0; PPeI 235.3- 250.0; PPpI 190.4–204.4; HBaI 27.2–28.5.

Material examined: **Dominican Republic**: Constanza, 3–4,000 ft., August, 1938, 2 workers (holotype and paratype), DARLINGTON [MCZC]; Constanza to Jarabacoa, 2–4,000 ft., August 1938, 1 worker (paratype), DARLINGTON [MCZC].

Discussion. - *C. flavigaster* is the sister species of the copal species *taino*. Both species share the orange gaster and the irregular striation. KEMPF (1951) recorded the presence of two workers with reddish-orange gaster from Bizoton, Haiti, in the collection of the U. S. National Museum. He considered these specimens as "perhaps intergrades between *unimaculatus* and *vinosus*". One of the paratypes of *flavigaster* also shows a vestigial postero-median black strip on the first gastral tergite as the specimen from Bizoton mentioned by KEMPF (l. c.). We regard the specimens listed above as representing a good species for the unique possession of sinuous striation, first gastral tergite orange and pilosity sparse. Each of these three

Fig. 37. *Cephalotes flavigaster* DE ANDRADE. Worker from Constanza-Jarabacoa, Dominican Republic: head (top) and mesosoma (bottom) in dorsal view.

characters can be used to separate at glance *flavigaster* from *unimaculatus* and from *vinosus*, two species with more regular striae, with denser pilosity and with different gastral coloration.

We did not see the two specimens from Bizoton mentioned by KEMPF (1951), but they are likely to be close to or identical with *flavigaster*.

Distribution: Dominican Republic.

5.6.2. The *atratus* clade

This clade corresponds to the former genera *Cephalotes* and *Eucryptocerus*. It is characterised by two synapomorphies among the characters we tentatively retained for our data matrix: (1) the bispinose vertexal border, a character which, in this order of magnitude, is uniquely derived among the members of this group but appears to be paralleled by some (certainly homoplastic) denticles to be found among other species like *borgmeieri*, *betoi*, etc.; (2) the presence of a pair of dorsal pronotal spines, another character derived uniquely for the members of this clade but which appears to have been (?secondarily) lost among very small *atratus* and *opacus* workers. The absence of a soldier caste, which we stressed as a significant plesiomorphic trait of the *hamulus* clade, is still recognisable among some members of the *atratus* clade: there is at least one species certainly without morphologically differentiated soldiers (*atratus*) but the worker caste, in this case, is slightly polymorphic in size. Other species, like *oculatus* and *placidus*, are still known from too few specimens as to permit definitive conclusions about their polymorphism. The members of this clade are among the largest *Cephalotes*. Only some species of the *clypeatus* clade approach their size.

The *atratus* clade contains the following seven species: *alfaroi*, *atratus*, *marginatus*, *oculatus*, *opacus*, *placidus*, *serraticeps*.

Cephalotes atratus (LINNAEUS)

Figs. 38, 39, 40, 358, 359, 360

Formica atrata LINNAEUS, 1758: 581. Worker. Original description. Type locality: "America meridionalis". Type material not available for the present study.

Formica quadridens DE GEER, 1773: 609, pl. 31, fig. 17–20. Worker. Original description. Type locality: Surinam. Synonymy by RETZIUS, 1783: 76.

Cephalotes atratus, LATREILLE, 1802 a: 358. First combination in *Cephalotes*.

Formica atrata, LATREILLE, 1802 b: 272, pl. 12, fig. 74. Worker, gyne.

Cephalotes quadridens (DE GEER), SANTSCHI, 1919: 44. First combination in *Cephalotes*.

Cryptocerus dubitatus SMITH, 1854: 216, pl. 20, fig. 1. Male. Original description. Type locality: Brazil. Type material presumably lost (neither in the BMNH nor in OXUM). Synonymy by SMITH, 1858: 188.

Cryptocerus atratus ab. *rufiventris* EMERY, 1894 b: 4. Worker. Original description. Type locality: Tucumán (Argentina). Type material not available for the present study. Synonymy by KEMPF, 1951: 115.

Cryptocerus atratus, SHARP, 1899: fig. 74. Worker.

Cephalotes atratus var. *nitidiventris* SANTSCHI, 1920: 148. Worker. Original description. Type locality: Cayenne and Lumier River (French Guyana). Type material: 2 syntype workers labelled "America, Cayena 1905, E. Grouvelle" (sic) in NHMB, examined. Synonymy by KEMPF, 1951: 115.

Cephalotes atratus stirps *crassispina* SANTSCHI, 1920: 148. Worker. Original description. Type localities: Mato Grosso (Brazil), Formosa (Misiones, Argentina), and Santa Trinidad (Paraguay). Type material 3 workers from Urucuru, Mato Grosso (Silvestri), 3 workers from Formosa (Argentina, Joergensen), 1 worker from Paraguay without further data, all in NHMB, examined. Synonymy by KEMPF, 1951: 115.

Cephalotes atratus erectus (unavailable name by SANTSCHI, 1920, see Chapter 5.10), first available mention as trinomen by KEMPF, 1951: 124. Worker, gyne. New synonym.

Cephalotes atratus quadridens (DE GEER), WHEELER, 1936 a, fig. 1. Head of gynandromorph.

Cephalotes atratus LINNAEUS, EIDMANN, 1936: 81, pl. 1, figs. I 10 & VII 1–3. Egg, last instar larva.

Cryptocerus atratus LINNAEUS, BRISTOWE, 1941: fig. 67. Worker.

Cephalotes atratus (LINNAEUS), KEMPF, 1951: 114, figs. 95, 96, 97, 100, 104. Worker, gyne, male.

Cephalotes atratus (LINNAEUS), WHEELER & WHEELER, 1954 b: 154, figs. 18–28. Young and last instar worker larva, gyne larva.

Cephalotes atratus, KUGLER, 1978: 473, figs. 188–191. Worker, sting.

?*Zacryptocerus* spp., SEAR, 1996: 7. Worker (colour photograph).

Cephalotes atratus, OLIVEIRA & SAZIMA, 1984: fig. 5. Worker.

Cryptocercus (sic) *atratus*, PARKER & CLOUDSLEY-THOMPSON, 1986: fig. 1. Worker. Misspelling.

Cephalotes atratus, JAFFE C., 1993: pl. 11. Worker (colour drawing).

Diagnosis. - A member of the *atratus* clade differing from its sister species *marginatus* (q. v.) by the sparser pilosity on the ventral part of the gastral sternites of the worker and of the gyne, and, in the male, for the denser foveolation of the mesosoma and by the greater CI. Both sister species (*atratus* and *marginatus*) are among the largest of the genus and differ from closely related ones by the lack of crenulation on the posterior half of the frontal carinae.

Worker (Figs. 359, 360) (description of KEMPF, 1951). - "Monomorphic. Length 8–14 mm. Black; the following fuscous ferruginous: two semitranslucid spots on each frontal carinae, tips of tarsi.

Head subopaque; finely reticulate-punctate. Mandibles densely and finely rugose and punctured. Frontal carinae slightly diverging caudad, scarcely upturned laterad, vestigially crenulate anteriorly with only a few projecting setae, remaining part not crenulate and without setae. Occiput continuous with upper surface of head, inclined ventrad; its angles with a pair of spines. Vertex without spines nor swellings. Lower occipital border straight, carinulate. Upper surface of head and cheeks covered with sparse oval foveolae, containing a short, scale-like, silvery, decumbent hair. Lower surface of head more coarsely reticulate-rugose and foveolate. Apical segment of maxillary palpi somewhat longer than the preceding.

Thorax subopaque. Shoulders obtusely dentate. Scapular spines strong, obliquely inclined backward, and laterad, subacuminate, the apical half more or less recurved, with a small tooth projecting from the anterior face at the bent. Median pronotal spines usually minute, vestigial or absent. Promesonotum moderately longitudinally convex, immarginate laterad. Promesonotal suture distinct. Mesonotum flat, with a minute tubercle laterally toward the posterior angle. Mesoepinotal suture distinct and impressed. The basal face of the epinotum slightly inclined forward, immarginate laterad, slightly constricted in front of the oblique, more or less divergent, straight to slightly curved epinotal spines. Entire thorax finely reticulate-punctate, with sparse setigerous foveolae, crowded and more deeply impressed on pronotum, very sparse on the pleura, leaving free spaces, which are mostly longitudinally rugose. Mesopleura with a small tooth above the anterior corner of the mid coxae. Declivous face mostly without coarse sculpture. Outer surface of fore coxae transversely striated. Legs without foveolae, but with appressed setae. Oblique setae on apical end of femora, tibiae and on tarsi. Petiole shorter than broad, subcuboidal, denesely foveolate above and on the sides, with a small sidewards projecting tubercle or tooth on each anterior corner. Ventral face strongly keeled, ending anteriorly in an obtuse tooth. Postpetiole more than 1.5 times as broad as long. Sides with a conspicuous, anteriorly angulate, posteriorly rounded swelling, the sides converging caudad. Upper face flat, with a pair of small tubercles on the anterior border. Ventral face with a large, truncate, rounded or bifid lobe, projecting ventrad and somewhat cehalad. Sculpture as on petiole.

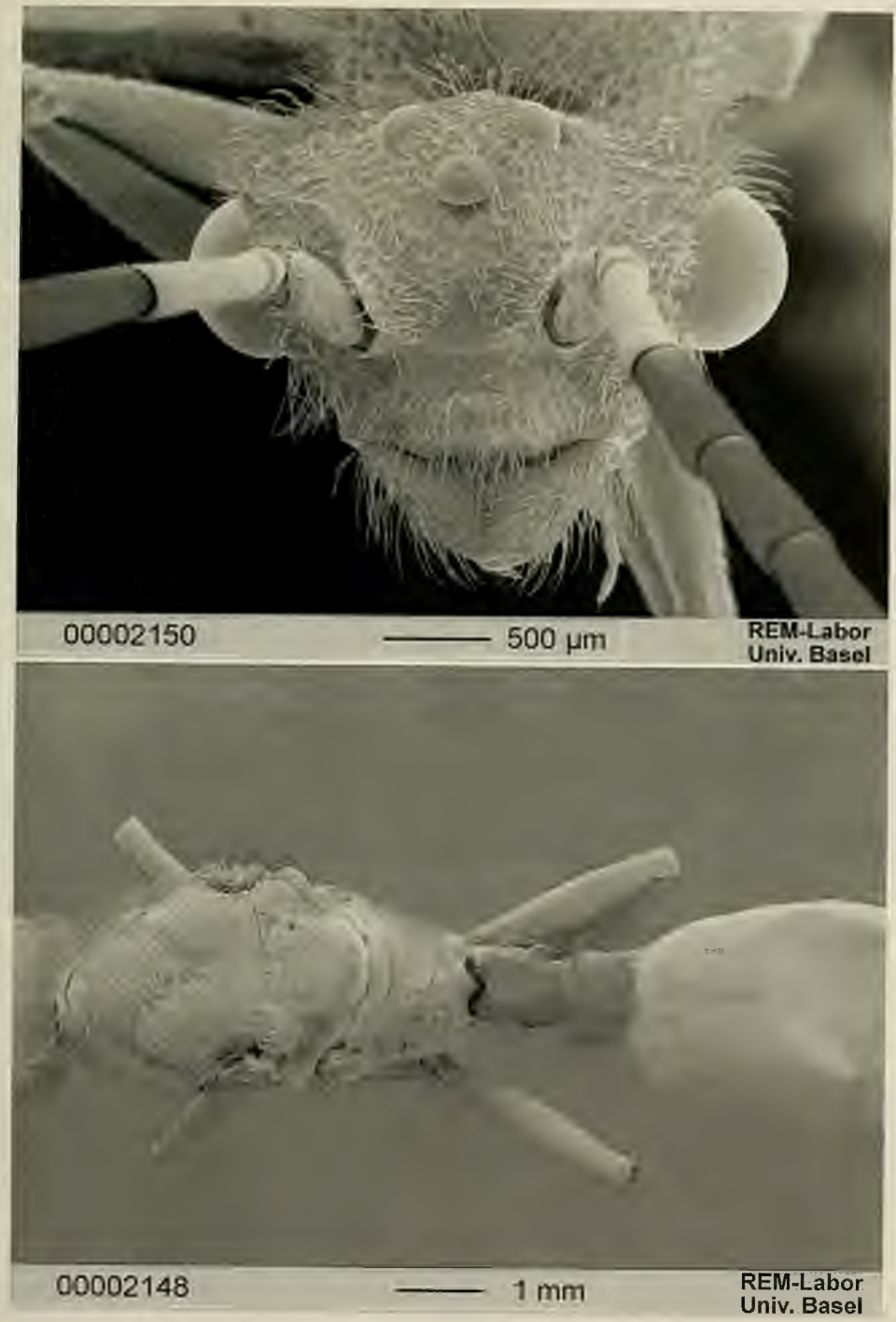


Fig. 38. *Cephalotes atratus* (LINNAEUS). Male from Manaus, Brazil: head (top) and mesosoma (bottom) in dorsal view.

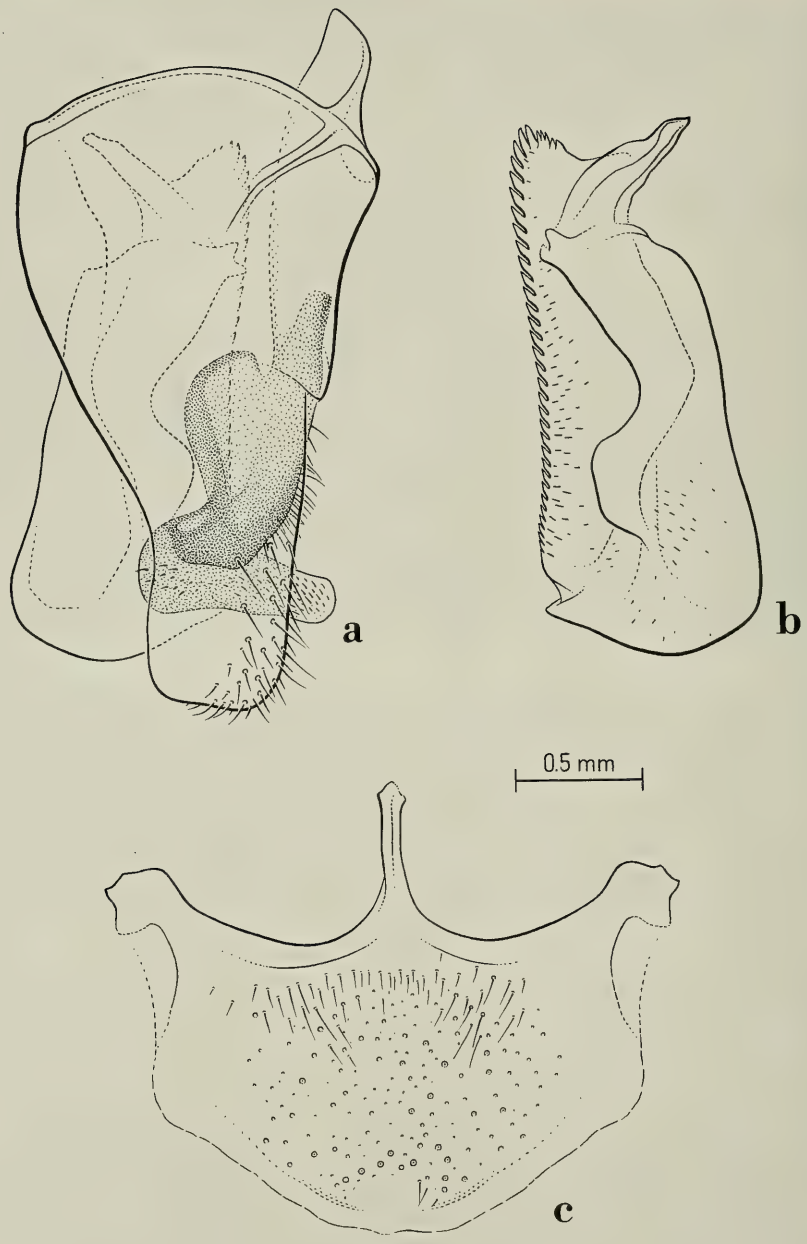


Fig. 39. *Cephalotes atratus* (LINNAEUS). Male from Manaus, Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Gaster elliptical, subopaque to subfulgid, finely reticulate-punctate, covered with larger, elongate, shallow grooves, containing a decumbent hair. Posterior half of first sternites and the exposed portion of the tergites and sternites 2–4 with sparse, suberect, pale-brownish hairs."

Measurements (in mm) and indices: TL 7.64–15.10; HL 1.60–3.30; HW 2.08–4.50; EL 0.48–0.80; PW 1.88–4.80; PeW 0.50–1.00; PpW 0.59–1.08; HBaL 1.32–2.30; HBaW 0.34–0.51; CI 130.0–136.4; PI 93.7–112.9; PPeI 349.3–480.0; PPpI 317.9–444.4; HBaI 22.2–25.7.

G y n e (Fig. 358) (description of Kempf, 1951). - "Length up to 23 mm. Somewhat similar to the worker. Black, subopaque. Head somewhat broader than long. Mandibles strongly rugose. Clypeus much broader than long, subtriangular. Frontal carinae distinctly converging anteriorly, not parallel not upturned laterally, slightly crenulate on anterior third, with a few projecting setae. Vertex with a pair of obtuse swellings, just in front of the subtruncate occiput. Occipital angles bituberculate. Cheeks immarginate below. Sculpture as in worker. Thorax subopaque. Pronotum immarginate cephalad and laterad. Shoulders low, bluntly angulate. Scapular spines short, stout, acute. Transverse crest of pronotum vestigial, not carinate, two median pronotal spines short, obtuse. Mesopleura with a small tooth above the mid coxa. Epinotum narrow, immarginate, laterad, spines short, icrassate at base, apices slightly diverging, their interapical distance less than 1/2 of the maximum width of thorax. Declivous face twice as long as basal face of epinotum. Sculpture as on head. Basitarsus of mid and hind leg flattened and broadened, not as thin as in worker. Petiole short, about twice as broad as long, the upper face presenting a transverse keel. Postpetiole longitudinally, greatly convex, with a large, blunt, rounded swelling laterad, about twice as broad as long. Ventral lobe less conspicuous than in worker. Both peduncular segments coarsely and rather densely foveolate. Gaster as in worker, more elongate, sides subparallel, the microsculpture less prominent; first tergite rather fulgid discad, sparsely foveolate, the foveolae smaller than on thorax and on head. Wings infumated. Fore wing with fuscous stigma and a dark streak along the subcostal vein. Marginal cell closed and appendiculate. Submarginal cell shorter than in *Zacryptocerus clypeatus*. Transverse cubital vein absent, the cubital vein touching the marginal cell. Second abscissa of subcostal vein shorter than the section of basal vein that encloses the submarginal cell. Occasionally stubs projecting from the cubital vein into the submarginal cell and the apical field."

Measurements (in mm) and indices: TL 15.06–19.50; HL 2.76–3.65; HW 3.32–4.50; EL 0.64–0.80; PW 2.60–4.50; PeW 0.96–1.40; PpW 1.16–1.60; HBaL 1.76–2.00; HBaW 0.486–0.60; CI 120.0–126.5; PI 93.3–127.7; PPeI 270.8–321.4; PPpI 224.1–281.2; HBaI 27.3–30.0.

M a l e (Fig. 38) (description of Kempf, 1951). - "Length 13.2 mm. Median head length 1.53 mm. Weber's length of thorax 4.05 mm. Black: the following brunneous: antennae, coxae, trochanters, base of femora. Orange-brown: gaster, femora, tibiae, tarsi.

Head, without mandibles much broader than long (103 : 63). Mandibles finely rugulose and punctate; chewing border with distinct apical and preapical tooth. Clypeus transverse, anterior face truncate, subperpendicular to upper surface of head, posterior half at right angles to it; horizontal. Anterior border straight, posterior border marked by a deep transverse depression in front of the antennal sockets. Entire clypeus finely shagreened. Frontal carinae scarcely expanded, divergent caudad, fading out before the posterior border of eye. Antennal scrobes indistinct. Ocelli on vertex, conspicuous, subequal to diameter of second funicular segment. First funicular segment shorter than broad. Second funicular segment longer than the following, except of the apical segment.

Thorax subopaque, almost twice as long as maximum width (83 : 47). Pronotum immarginate laterad, with a minute tooth on the anterior angle, and a longer blunt tooth somewhat behind; rugose-reticulate and foveolate. Scutum convex with deeply impressed Y-shaped Mayrian furrows, antero-mesal part deeply and densely foveolate, postero-lateral portion more sparsely and shallowly foveolate. Scutellum similarly sculptured with anterolateral lobes almost constricted off by a deep transverse furrow immediately behind the anterior border. Basal face of epinotum shorter than declivous face, transversely convex, immarginate

laterally, posterior corners with a sharp carinule, reticulate-rugose and foveolate. Declivous face finely reticulate, subfulgid, with a few faint, distinct rugulae. Sides of mesothorax finely shagreened anteriorly, sparsely, shallowly foveolate and rugose posteriorly. Basitarsi elongate, compressed.

Petiole subopaque, slightly broader than long, anterior face truncate, excavate, the sides somewhat converging behind, finely shagreened above, finely longitudinally rugose laterad, and reticulate-rugose antero-laterad. Postpetiole broader than long, sides greatly convex, subtuberculate, sculptured as petiole.

Gaster subopaque, short, fusiform, finely shagreened. Subgenital plate transverse, apical border rounded.

Genitalia and subgenital plate as in Fig. 39.

Wings (Fig. 40) leathery, infumated. Veins brunneous. Fore wings with fuscous stigma, and fuscous streak along the subcostal vein. Marginal cell closed and appendiculate. Discoidal cell extremely small. Transverse cubital vein present, cubital vein not touching the marginal cell.

Pilosity gold-brown. Antennae with dense fine pubescence. Long dense hair on head and thorax; sparse, appressed on first gastral tergite, erect on apical border of the gastral tergites and sternites.

Certain features are highly variable, even among males of the same nest. Among those are the occipital spines, which may form mere perpendicular carinule on each side, or even be quite obsolete. The same is true for the carinules on the posterior corner of the epinotum, which may be occasionally tooth-like. The sculpture in some instances is coarser than in the specimen described above. The following variability occurs in the fore wing: discoidal cell always small, sometimes minute, open or even completely absent. Stubs projecting into submarginal cell from various places of the recurrent and the cubital veins."

Measurements (in mm) and indices: TL 9.78–13.21; HL 1.28–1.68; HW 1.68–2.16; EL 0.53–0.70; PW 1.60–2.24; PeW 0.72–0.92; PpW 0.88–0.96; HBaL 1.32–1.84; HBaW 0.18–0.26; CI 128.3–131.9; PI 96.4–105.0; PPeI 227.3–272.2; PPpI 208.3–233.3; HBaI 13.3–15.1.

Material examined. - **Belize**: Benque Viejo, 1 worker, Father STANTON [MCZC], a doubtful record as already written by KEMPF (1951: 119).

Costa Rica: Guápiles, 1915, 1 worker, D. E. HARROWER [MCZC].

Panama: no further locality, 1 worker, MAR. WAGN. [ZSMC]; Barro Colorado Is., Canal Zone, 1938, 1 worker [MCZC]; same locality, 20.VI. and 24.VII.1924, 5 workers, W. M. WHEELER [MCZC]; same locality, 14–22.VII.1924, 5 workers, 2 gynes, N. BANKS [MCZC]; same locality, 1 worker, P. RAU [MCZC]; same locality, Aug. 1930, 1 worker, C. P. HASKINS [MCZC]; same locality, 1938, 1 worker, N. A. WEBER [MCZC]; same locality, 2 workers, W. C. ALLEE [MCZC]; same locality, I. 1960, 1 worker, W. L. BROWN & E. S. MCCLUSKEY [MCZC]; Canal Zone, Ancon, 09.VII.1924, 1 worker, N. BANKS [MCZC]; 4 mi NW Gamboa, 23.II.1975, 3 workers, LAWRENCE & ERWIN [MCZC]; Bella Vista, 06.VII.1924, 1 worker, N. BANKS [MCZC]; Monte Lírio, 18.XI.1911, 3 workers, W. M. WHEELER [MCZC]; Punto Paitea, 07.II.1924, 3 workers, W. M. WHEELER [MZSP]; Darien, 2 workers (syntypes of the var. *erecta*), F. GEAY [NHMB].

Colombia: no further locality, 3 workes [MHNG]. Limón Cocha and Vic. Ecuador, Sept. -Nov. 1964, 5 workers, H. R. HERMANN [MCZC]. Guajira: Dibulla, 7 workers [MHNG]. Magdalena: Aracataca, 20.V.1921, 1 gyne, DARLINGTON [MCZC]; Río Frío, 8 workers, G. SALT [MCZC]; same locality, XI.1911, 1 worker [MCZC]. Cundinamarca: Bogotá, Landarvri, 1100 m, 19.VII.1941, 2 workers, L. RICHTER [MCZC]. Valle: Sevilla, 12.VII.1926, 2 workers, [MCZC]; Villavicencio, Ap. Maria, XII.1928, 1 worker [MZSP]. Amazonas: La Chorrera, 30 km downhill Río Igara Paraná, 17.XII.1973, 01.II, 10.II, 15.II, 20–24.II, 26.II, 25.III. 26 workers, J. DESPLATS [MNHN]; La Chorrera, 50 km downhill Plateau de Grés, Adofiki, 06–10.X.1073, 4 workers, J. DESPLATS [MNHN]; La Chorrera, 05.VIII.1920, 4 workers, Cornell Univ. Exp. [MZSP]; Leticia, 23.VIII, Oct. -Nov. 1973, 9 workers, M. CORN [MCZC]; same locality, VIII.1974, 2 workers, 1 gyne, M. L. CORN [MZSP]; Witoto Aimeni Unoniai, 19.XII.1973, 6 workers, J. DESPLATS

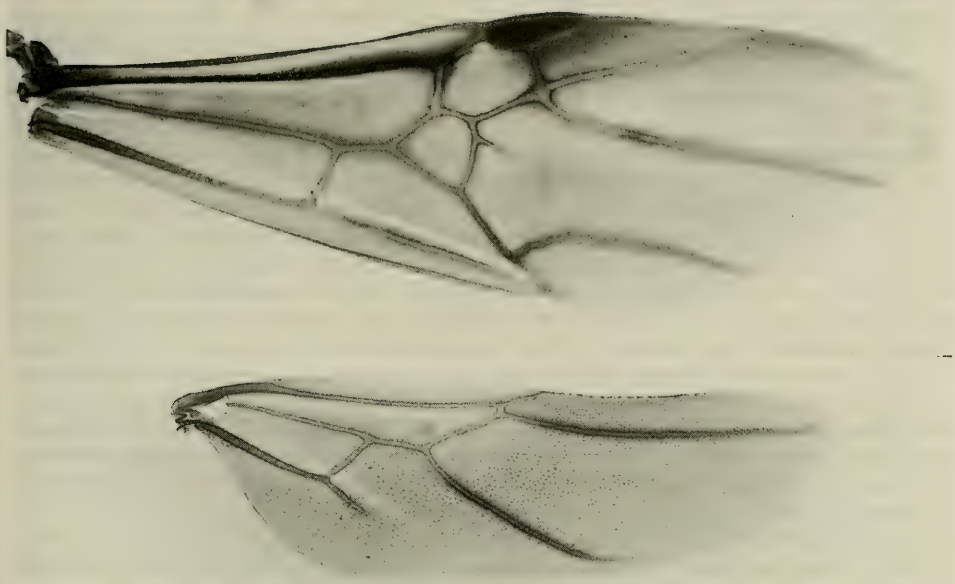


Fig. 40. *Cephalotes atratus* (LINNAEUS). Male from Manaus, Brazil, fore and hind wings.

[MNHN]; 18 km N of Leticia, 28.II.1974, 5 workers, S. & J. PECK [MCZC]; Sasaima, 1 worker, APOLINAR M. [MZSP]. Antioquia: Cocorna, La Veta Orillos, Caño La Granja, 2 workers, F. FERNÁNDEZ [MZSP]. Vaupés: Río Tiquie, 1 worker (red gaster!), M. CREAGH [MZSP].

Venezuela: Carisco, 1896, 1 worker, "*E. crassicorne* and *C. atratus* in figth" [MHNG]; Anduze, 02.XII.1939, 1 worker [MCZC]. Zulia: Los Angeles del Tucuco, 15–16.IV.1981, 1 worker, A. S. MENKE & L. HOLLENBERG [USNM]. Aragua: 2 km N Ocumare De La Costa, 21–22.VI.1976, 1 worker, A. S. MENKE & D. VINCENT [USNM]. Guárico: Hato Masaguaral, 44 km S Calabozo, 03–10, 11–19.V.1985, 4 workers, 4 gynes, MENKE & CARPENTER [USNM]. Barinas: 10 km NW Barinas, 280 m, 14.I.1985, 6 workers, C. VOGT [MCZC]. Bolívar: Caicara, Rio Orinoco, 4 workers [MCZC]. Amazonas: Orinoco Delta, I-II.1935, 6 workers, N. A. WEBER [MCZC]. Carabobo: San Esteban, 27.IX.1937, 5 workers, G. VIVAS-BERTHIER [MZSP]. Miranda: Estación Experimental Rio Negro, 100 m, 17–19.VI.1980, 4 workers, J. A. CLOVIJO & A. CHACON [MPEG]; Campo Central de Caucagua, 15–16.III.1982, 7 workers, C. R. F. BRANDÃO, J. VALENZUELA & P. JAISSON [MZSP]. Cojedes: Chaparral, 10 km W H. Piñero, ca. Baúl, 22.X.1986, 2 workers, E. M. CANCELLO & C. R. F. BRANDÃO [MZSP]. Sucre: El Ricón, 30 km S Carupano, 10° 36' N 83° 12' W, 01.XI.1986, 1 worker, E. M. CANCELLO & C. R. F. BRANDÃO [MZSP]; Cariaco, 29.I.1910, 1 worker [NHMB].

Trinidad & Tobago: Trinidad: no further locality, 26 workers [MHNG]; no further locality, 2 workers, URICH [MHNG]; no further locality, 9 workers, FOREL [MHNG, NHMB]; no further locality, 6 workers, WHEELER [MCZC]; Port of Spain, 1913, 4 workers, R. THAXTER [MCZC]; same locality, 9 workers, 13.I.1910, F. B. WHELPLEY [MCZC]; Cumuto, 24.IV.1929, 2 workers, DARLINGTON [MCZC]; St. Augustine, 16.XI.1934, 4 workers

[MCZC]; same locality, 04.VIII.1935, 30.IX.1935, 21–22.V.1936, 25 workers, N. A. WEBER [MCZC]; same locality, 20–30.IV.1929, 2 workers, DARLINGTON [MCZC]; Nariva Swamp, 10.III.1935, 1 worker, N. A. WEBER [MCZC]; Mt. Tucuche, IV.1929, 1 worker [MCZC]; Maracas Valley, 26 & 28.V.1936, 8 workers, N. A. WEBER [MCZC]; nr. Río Claro, 01.VI.1936, 1 worker, N. A. WEBER [MCZC]; Broad Bay, 01.VI.1989, dry river bed, 1 worker, JPEC, DARLINGTON [MCZC].

Guyana: Bartica, 15–20.IX.1917, 3 workers, WM. BEEBE [MCZC]; Kartabo, Jul.-Aug. 1920, 67 workers, 4 males, W. M. WHEELER [MCZC]; Georgetown, 07.IV.1920, 2 workers, W. M. WHEELER [MCZC]; same locality, 09.VI.1936, 2 workers, N. A. WEBER [MCZC]; same locality, 02.VI.1911, 1 worker [MCZC]; same locality, 2.VII.1911, 1 worker, LUTZ [MCZC]; Kamakusa, 8 workers, H. O. LANG [MCZC]; Barakara, 05–20.VII.1920, 2 workers, 3 males, W. M. WHEELER [MCZC]; Wanamu R. 6 workers, W. J. LAVARRE [MCZC]; Camaria, 28.VII.1920, 3 workers, W. M. WHEELER [MCZC]; Paxarampa Mt. 1 worker, M. J. LAVARRE [MCZC]; Canister Falls, Nov. 1921, 3 workers [MCZC]; between R. Cuyuni and R. Mazaruni, 1 worker, N. A. WEBER [MCZC]; Rio Essequibo, 1 worker, J. OGILVIE [MCZC].

Surinam: Kabel, 19.X.1958, 5 workers, P. H. V. DOESBURG [MZSP]; Paramaribo, 4 workers, BUENZLI [MZSP]; Christian Kondre, Marowijne Distr., XII.1963, 10 workers, B. MALKIN [MZSP]; area of the Lucie River, 07.VIII.1926, 1 worker, Surinam Expedition [NHMB]; Brokopondo, Saramaca R. left side, 30 km above Kwakoegron, 10.XII.1961, 1 worker, K. KRISHNA [MCZC].

French Guyana: without further locality, 2 gynes [MHNG], 1902, 1 worker, E. RECH [NHMB]; Cayenne, 1905, 2 workers (syntypes of the var. *nitidiventris*), E. GROUVELLE [NHMB]; same locality, no further data, 1 worker [NHMB]; Maroni, 2 workers, LE MOULT [NHMB]; St. Jean du Maroni, 04.V.1914, 2 workers, 1 gyne, R. BENOIST [NHMB]; Camopi, 1900, 1 worker, F. GEAY [NHMB]; Nouveau Chantier, July, 1 male, LE MOULT [NHMB]; Riv. de Kourou, 2 workers, LE MOULT [NHMB] Maripasoula, 7.XII.1963, 3 workers, B. MALKIN [MZSP]..

Ecuador: Z a m o r a C h i n c h i p e : Between Río Bom Boiza and Río Zamora, 08.XII.1934, 2 workers, W. VON HAGEN [MZSP]; same locality, 12.VIII.1934, 6 workers [MCZC]. P i c h i n c h a : Quito, 1 worker, 1 gyne, E. NAUMANN [MHNG]. N a p o : Mishualli, 5.X.1987, 4 workers, M. HUYBENSZ [MCZC]; same locality, 29.VI.1976, 1 worker, C. TARRANT [MCZC]; Coca, V.1965, 5 workers, 2 gynes, L. PEÑA [MCZC]. M o r o n a S a n t i a g o : Gualaquiza, 01.VII.1935, 1 worker, W. VON HAGEN [MCZC]; same locality, 29.X.1934, 1 worker, W. VON HAGEN [MZSP]; same locality, 1 worker [MCZC]. Los Tajos, 03.VIII.1976, 1 worker, TJITTE DE VRIES [MZSP].

Peru: Llinguipata, 2 workers, N. HOLMGREN [MCZC]; Azupizu, Cam. del Pechis, 08.VI.1920, 1 worker [MCZC]; Valle Chanchamayo, 800 m, II.1939, 1 worker, W. WEYRAUCH [MZSP]. L o r e t o : Upper Marañón, 2 workers, ORTON [MCZC]; Iquitos, 1 gyne, STAUDINGER [MCSN]; Callicebus Res. Station, Mishana, Río Nanay, 25 km SW Iquitos, 120 m, 10–17.I.1980, 1 worker, J. B. HEPPNER [USNM]; Erstirón, Río Apiaçu, 15.V.1966, 3 workers, B. MALKIN [MZSP]. H u á n u c o : Tingo María, 670 m, 2 workers, W. WEYRAUCH [MZSP]. A n c a s h : Chancos, 1 worker [MCSN]. M a d r e d e D i o s : Río Tambopata Res. 30 km SW Puerto Maldonado, 290 m, 12°50' S 69°20' W, 09.III.1982, 1 worker, T. L. ERWIN et al. [MCZC]; same locality, 12°51' S, 69°17' W, 22–25.I.1985, 2 workers, J. CARPENTER & D. BOWERS [MCZC]; same locality, 290 m, 02–05.XI.1979, 1 worker, J. B. HEPPNER [USNM]; Cocha Cashu, Tambopata Prov. 19.VIII.1982, 2 workers, F. WHITE [MCZC]. C u z c o : Cuzco, 22.X.1964, 1 worker, P. COBATA [MZSP]; Marcapata, 2 workers [MCZC]; Quincemil, 750 m, IX.1962, 1 worker, L. PEÑA [MCZC]; Cachobi, 2 workers, ROSENBERG [MZSP]. N a p o : Limoncocha, 0°24' S, 76°36' W, 4.11.1967, 16.VI.1970 & 29.VI.1972, 5 workers, C. W. & M. E RETTENMEYER, P. L. KAZAN [MZSP]. J u n í n : Colónia del Perené, Pueblo Pardo, 17.I.1920, 2 workers [MZSP]; La Merced, 1 worker [MZSP]. U c a y a l i : Río Alto Purús, 1000 m, 14.IX.1960, 1 worker, W. WEYRAUCH [MZSP]; Río Paucartambo, 800 m, 15.IX.1960, 1 worker, W. WEYRAUCH [MZSP].

Brazil: no further locality, 3 workers [NHMB]. R o r a i m a : Rio Uraricuera, Ilha Maraca, III.1976, 3 workers, R. NEGRETT [MZSP]; same locality, 18–23.VIII.1987, 1 worker,

J. S. RAFAEL et al. [INPA]. A m a p á : Santana, Rio Amazonas, 14.VI.1966, 4 workers, W. WEYRAUCH [MZSP]; Serra do Navio, 23.IX–06.X.1957, 23 workers, K. LENKO [MZSP]; same locality, 7.II.1980, 9 workers, P. CELSO & E. L. Oliveira [MPEG]; Highway BR. 156, km 14, 9.XII.1982, 1 worker, M. F. TORRES [MPEG]; Porto Platon, X.1957, 1 worker, K. LENKO [MZSP]; Oiapoque, 2.V.1979, 6 workers, W. L. OVERAL [MPEG]; Macapá, 5.V.1979, 5 workers, W. L. OVERAL [MPEG]; Macapá-Pacoval, 20.X.1978, 1 worker, M. F. TORRES [MPEG]; Pacoval, Fazenda Sr. Durval, 17.XI.1981, 1 worker, GORAYEB et al. [MPEG]; Porão Grande, 5.IV.1979, 1 worker, P. CELSO [MPEG]; same locality, 5.IV.1980, 2 workers, HIGINO & NONATO [MPEG]; Mazagão, 24.IX.1981, 1 worker, GORAYEB et al. [MPEG]; same locality, Fazendinha, 9.XI.1978, 2 workers, M. F. TORRES [MPEG]. A m a z o n a s : no further locality, 1 gyne, 1 male, H. W. BATES S. [ZSMC]; no further locality, 1 worker, ROMAN [MCZC]; Taperinha, Santarém, 21–30.VI.1927, 3 workers, ZERNY [MCZC]; Rio Autaz, 1 worker, ROMAN [MCZC]; Mouth of Rio Negro, 18–24.IX.1912, 2 workers, HASEMAN [MCZC]; Manaus to Itacoatiara Highway, km 34, 07.VI.1971, 1 worker, W. L. & D. E. BROWN [MCZC]; Manaus, 13.III.1982, 1 worker, F. W. MORAES [INPA]; same locality, different dates and different collectors, 23 workers [MZSP]; BR 174, km 44, 25.II.1983, 2 workers, A. Y. HARADA [INPA]; BR 174, km 40, 14.III.1990, 1 gyne, A. Y. HARADA [INPA]; BR 174, km 44-EEST, 22.XI.1992, 17.VI.1994, 2 workers, A. Y. HARADA [INPA]; BR 174, km 54, 19.IX.1989, 1 worker, A. Y. HARADA [INPA]; same locality, km 70, II.1976, 1 gyne, V. P. DANIEL [MZSP]; Res. Flor. A. Ducke 2°55'S, 59°59'W, 27.VII.1994, 1 worker, ADIS et al. [INPA]; same locality, different dates between 1965 and 1969, 9 workers, VANZO [MZSP]; same locality, 02.X.1987, 1 worker, C. R. F. BRANDÃO [MZSP]; same locality, 24.II.1974, 1 gyne, L. P. A. [INPA]; same locality, 22–26.I.1996, 8 workers, 2 males, M. L. DE ANDRADE [INPA]; Manaus, Tropical Hotel Gardens, 8–10.XII.1984, 6 workers, J. C. TRAGER [MZSP]; Serra da Neblina, Rio Tucano, 230 m, 4.XII.1965, 1 worker, E. DENTE [MZSP]; Taracuá, Rio Uaupés, VIII.1964, 5 workers (with red gaster!), PEREIRA & MACHADO [MZSP]; Anavilhanas, left side of the Rio Negro, 21.IV.1967, 6 workers, Exp. Dep. Zool. [MZSP]; Rio Preto da Eva, near the mouth, 2.IV, 15.VI.1967, 11 workers, Exp. Perm. Amaz. [MZSP]; Porto América, Rio Putumayo, 30.VIII–02.X.1920, 1 worker, CORNELL exp. [MZSP]; Alto Parú, XI.1928, 3 workers, SAMPAIO [MZSP]; Lábrea, VIII.1970, 6 workers, G. GIRARDI [MZSP]; Tabatinga, X.1958, 4 workers, F. M. OLIVEIRA [MZSP]; Tefé, I.1962, 10 workers, R. CARVALHO [MZSP]; S. Gabriel, Rio Negro, X.1927, 3 workers, ZIKAN [MZSP]; Ituxi, Alto Purus, VIII.1971, 2 workers, J. BORRELLAS [MZSP]; Boca do Rio Purus, left side, 02–05.IV.1967, 1 worker, Exp. Perm. Amaz. [MZSP]; Igar. Barumunzinho, N of Manaus, 30.IX.1987, 1 worker, C. R. F. BRANDÃO & J. M. DINIZ [MZSP]; Esteirão do Equador, R. Javari, X.1979, 1 worker, ALVARENGA [MZSP]; Humaitá, A.C.A.R., 28.IV.1975, 4 workers, V. P. DA SILVA & A. DILLON [MZSP]; Itacoatiara, 1 worker, 1 gyne, DIRINGS [MZSP]. P a r á : no further locality, 3 workers [MHNG]; no further locality, 4 workers, G. FRANCK [MCZC]; no further locality, 1 worker, Thayer Exp. [MCZC]; no further locality, 2 workers [MCSN]; no further locality, V.1927, 2 workers, IX.1928, 2 workers, SAMPAIO [MZSP]; Igarapé, Belém, near Rio Solimões, 10.IV.1966, 1 worker, B. MALKIN [MZSP]; Serra Norte, Salabo, 20–25.VIII.1984, 1 worker [MPEG]; Serra Norte, Caldeirão, different dates and collectors, 17 workers [MPEG]; Rio Tapajós, 2 workers, E. SNETHLAGE [MPEG]; Monte Dourado, 29.X–2.XI.1979, 10 workers, R. B. NETO [MPEG]; Barcarena, 22.I.1984, 2 workers, P. C. SOUZA [MPEG]; S. S. Boa Vista, 5.IX.1982, 1 worker, W. OVERAL [MPEG]; Acará, 7.XII.1977, 1 worker, W. L. OVERAL [MPEG]; Paragominas, 02.VI.1966, 1 worker, P. PEREIRA [MZSP]; Santarém, VI.1920, 2 workers, J. GARBE [MZSP]; same locality, 1 worker, Thayer Exp. [MCZC]; Santarém, Fazenda Tapeirinha, II.1968, 8 workers, 1 gyne, Exp. Perm. Amaz. [MZSP]; same locality, 2°54' S, 54°20' W, 16.VI.1975 & 23.IX.1980, 5 workers, R. L. JEANNE [MZSP]; same locality, July, 1975, 6 workers, R. L. JEANNE [MCZC]; Benevides, different dates and collectors, 14 workers [MPEG]; Peixe Boi, 21–25.IV.1978, 2 workers, F. F. RAMOS & M. F. TORRES [MPEG]; Mocambo, different dates and collectors, 11 workers [MPEG]; S. M. do Guamá, 25.II.1987, 2 workers, J. DIAS [MPEG]; Taperinha, 40 km E Santarém, 25.X.1968, 1 worker, R. L. JEANNE [MCZC]; Aldeia Araçu, Igar. Urupi-Una, 31.I.1963, 1 worker, B. MALKIN [MZSP]; Jacareacanga, X.1959, 2 workers, 1 male, M. ALVARENGA [MZSP]; Alegre, 15 km NE Marapanin,

10.IX.1965, 1 worker, Exp. Dep. Zool. [MZSP]; Vizeu, 27.V.1978, 1 worker, W. L. OVERAL [MPEG]; Ourém, 29.X.1990, 3 workers, P. TADEO [MPEG]; Bujaru, 20–21.IV.1979, 12 workers, R. B. NETO [MPEG]; São Francisco, 14.I.1978, 10 worker, M. F. TORRES [MPEG]; Ponta de Pedras, 3–6.III.1979, 24 workers, W. FRANÇA & N. F. TORRES [MPEG]; Tucuruí, surroundings of the river, different dates and collectors, 43 workers [MPEG]; Paragominas, Fazenda Cachoeira, Rio Vermelho, 15–21.I.1991, 6 workers, P. TADEO [MPEG]; Serra Norte, Manganês, different dates and collectors, 22 workers [MPEG]; Serra Norte, Carajás, VII-VIII.1985, 7 workers, C. R. F. BRANDÃO & W. BENSON [MZSP]; Serra Norte, Rio Gelado, 19.IX.1985, 4 workers, M. ZANUTO [MPEG]; Serra Norte, Fofoca, different dates and collectors, 11 workers [MPEG]; Serra Norte, 3 Alfa, 26.VI & 1.VII.1985, 5 workers, H. ANDRADE & N. BITTENCOURT [MPEG]; Serra Norte, Cerrarias, different dates, 4 workers [MPEG]; Serra Norte, Estação Bahia, 14.IX.1985, 2 workers, W. FRANÇA [MPEG]; Gorotire-Xingu, X.1977, 1 worker, D. A. POSEY [MPEG]; Santa Julia, 23.I.1936, 2 workers, W. ADAMS [NHMB]; Alter do Chão, Rio Tapajós, 21–23.II.1968, 8 workers, Exp. Perm. Amaz. [MZSP]; Serra Cipó Pitanga, low Xingu River, 25–30.XI.1983, 3 workers, B. MASCARENHAS [MPEG]; Conceição do Araguaia, 12–21.XI.1979, 2 workers, W. L. OVERAL & P. MAURICIO [MPEG]; Bragança, 26 & 28.V.1978, 2 workers, M. F. TORRES & W. L. OVERAL [MPEG]; Soure, 25.II.1979, 1 gyne, S. A. SANTOS [MPEG]; Anajás, 7.IX.1982, 1 worker, W. L. OVERAL [MPEG]; Oriximiná, 13.I.1968, 4 workers, Exp. Perm. Amaz. [MZSP]; Cachoeira do Espelho, Rio Xingu, 21–28.X.1986, 1 worker, F. C. VAL [MZSP]; Belém, 12–19.VIII.1962, 3 workers, K. LENKO [MZSP]; same locality, 03–07.X.1964, 20 workers, P. E. VANZOLINI [MZSP]; same locality, 17.I.1959, 2 workers, P. WEIL [MZSP]; same locality, IX.1955, 2 workers, MARTINEZ [MZSP]; Belém, I. A. N., IX.1969, 18 workers [MZSP]; Belém, Reserva Guamá, APEG, 28.9–25.XI.1966, 9 workers, [MZSP]; same locality, 09.IV, 28.XI.1969, 7 workers, N. ROSA [MZSP]; Utinga, 02.II.1962, 1 worker, J. BECHYNÉ [MZSP]; same locality, different dates and collectors, 13 workers [MPEG]; Utinga, tract. near Belém, 06–07 VIII.1962, 3 workers, P. F. DARLINGTON [MCZC]; Belém, Fazenda Velha, 10.I.1979, 32 workers, W. FRANÇA, A. F. RAMOS & F. F. RAMOS [MPEG]; Itaituba, Parque Nacional da Amazônia, 13–14.XI.1978, 25 workers, W. L. OVERAL [MPEG]; São João de Pirabas, Japerica, 18–22.XII.1992, 7 workers, J. DIAS [MPEG]; São João de Pirabas, B. Esperança, different dates and collectors, 7 workers, [MPEG]; Primavera, 18.II.1987, 2 workers, M. ZANUTO [MPEG]; Primavera, B. Vista, Ilha Arapiranga, 20–30.XI.1992, 3 workers, J. DIAS [MPEG]; Óbidos, XII.1920, 3 workers, GARBE [MZSP]; Ó bidos, Traíra, 1 worker, DIRINGS [MZSP]; Óbidos, lower Amazonas, 15.I.1963, 15 workers, DIRINGS [MZSP]; Canindé, Rio Gurupí, X.1964, 27.II.1966, 12 workers, B. MALKIN [MZSP]; Aldeia Coraci, 11 km W Canindé, Rio Gurupí, XII.1964, 1 worker, B. MALKIN [MZSP]; boca do Cuminá-Miri, Oriximiná, 19–26.I.1968, 9 workers, Exp. Dep. Amaz. [MZSP]; Municipio Rio Tinto, Piabuçu, 15.II.1962, 1 worker, J. EVANGELISTA [MZSP]; Cachimbo, different dates, 7 workers, M. ALVARENGA et al. [MZSP]; Cachoeira do Tronco, Rio Cuminá, 05.IX.1936, 1 worker, ALMEIDA [MZSP]; Ilha Mexiana, aus Bambus, 9 workers, 5 gynes, HAGMAM [MHNG]. M a r a n h ã o : Barra do Corda, 17.VI.1966, 8 workers [MZSP]; same locality, 12.VI.1978, 1 worker, M. F. TORRES [MPEG]; Alto Turiaçu, Aldeia Gurupiuna, 16–19.II.1990, 8 workers, H. QUEIROZ [MPEG]; Rio Maracaçume, 22–23.V.1963, 1 gyne, B. MALKIN [MZSP]; Açailândia, P. Maranhão, 24.IX.1986, 10 workers, different collectors [MPEG]; Grajaú, R. Santana, 15.VI.1966, 8 workers, E.P.A. [MZSP]; Cajazeiras, 17.VI.1966, 2 workers, H. REICHARDT [MZSP]; S. Luís, 15.I.1959, 2 workers, D. WEIL [MZSP]. P i a u í : 20 km S Floriano, Buriti Sol, 05–12.XII.1991, 18 workers, 1 gyne, C. R. F. BRANDÃO & P. MOUTINHO; 10 km N Corrente, Fazenda Maracujá, 23–27.XI.1991, C. R. F. BRANDÃO [MZSP]; Rio Urucú-Preto, 20.II.1976, 4 workers, R. NEGRETT [MZSP]; Estação Ecológica Uruçuí-Una, 2 workers, GONÇALVES [MPEG]; Ribeirão Gonçalves, Estação Experimental Uruçuí-Una, cerrado, 06.XII.1980, 07.XII.1982, 12 workers, A. J. ALMEIDA FILHO [MZSP]; Lago Jacaré, Manacapuru, 26–28.III.1963, 5 workers, B. MALKIN [MZSP]. P a r a í b a : João Pessoa, VII.1955, 1 worker, P. PEREIRA [MZSP]; João Pessoa do Buraquinho, IBDF, 25–29.I.1989, 8 workers, A. L. HENRIQUES & F. F. RAMOS [MPEG]. P e r n a m b u c o : Olinda, 1 worker [MHNG]; Itamaracá, Eng. S. João, 07–10.V.1971, 8 workers, Exp. ABC & MZSP [MZSP]; Tapera, 4 workers, PICKEL [MZSP]. A c r e : Cruzeiro do Sul,

XII.1963, 2 workers, P. L. HERBEST [MZSP]; same locality, 12.VII, 19.X.1983, 9 workers, F. H. CAETANO [MZSP]; same locality, 07.VI, 14.VII.1983, 5 workers, R. H. PIRES [MZSP]; Iquiri, IX.1951, 1 worker, Exp. D. Zool. [MZSP]; Porto Valter, X.1961, 2 workers, P. L. HERBEST [MZSP]; Vila Taumaturgo, II.1962, 6 workers, P. L. HERBEST [MZSP]; Rio Branco, different dates and collectors, 55 workers [MPEG]; Rio Branco, Parque Zoobotanico, Cidade Universitaria, 28.II.87, 8 workers, E. DEUS [MZSP]; Porto Acre, Humaitá, 25.VI–2.VII.1992, 84 workers, GORAYEB et al. [MPEG]; Feijó, XII.1956, 6 workers, W. BOKERMANN [MZSP]. Rondônia: Ji-Paraná-Gleba, Sitio Novo Horizonte, 20–23.II.1983, 1 worker, J. ARIAS [INPA]; Porto Velho, 03.III.1979, 1 gyne, D. NEED [INPA]; Porto Velho, Guaporé, XI.1954, 6 workers, F. S. PEREIRA, E. DENTE, M. ALVARENGA & WERNER [MZSP]; 378 km S Porto Velho, 25.I & 9.II.1961, 3 workers, PEREIRA & MACHADO [MZSP]; Posto Industrial 7 de Setembro, VII.1980, 1 worker, C. E. A. COIMBRA [MZSP]; F. Principe da Beira, 10.XI.1961, 1 worker, F. M. OLIVEIRA [MZSP]; Alto Paraíso, 26.X, 02.XI.1986, 5 workers, Museu Polonoroeste [MZSP]; Nova Brasilândia, 15–19.XI.1985, 1 worker, Museu Polonoroeste [MZSP]; Ig. Marmello, Rio Abunã, XI.1962, 8 workers, WERNER & BOKERMANN [MZSP]; 5 km SW Sta Cruz da Serra, 04–10.XI.1985, 26 workers, Museu Polonoroeste [MZSP]. Goiás: Campinas, 1 worker, 1 gyne, SCHWARZMEIER [MZSP]; Anápolis, km 46 on rd. to Goiania, 10–12.V.1971, 2 workers, W. L. & D. E. BROWN [MCZC]. Distrito Federal: Brasilia: 10.IV.1965, 2 workers, W. E. TRIPLEHORN [MCZC]; Brasilia, 1 worker, 2 gynes [ZSMC]; Reserva Biológica de Águas Emendadas, 27–30.VI.1991, 42 workers, C. R. F. BRANDÃO, M. F. FRANÇOSO & A. A. REIS [MZSP]; E. Ecol. Águas Emendadas, different dates between March and November 1992, 47 workers, A. A. REIS [MZSP]; Parque Nacional de Brasilia, 13–14.V.1971, 3 worker, W. L. & D. E. BROWN [MCZC]. Minas Gerais: no further locality, 14 workers, E. LUJA & E. GARBE [MZSP, NHMB]; 1897, 1 gyne [MCSN]; Fátima S. Lourenço, 13.VI.1952, 1 worker, GILBERT & MÜLLER [MZSP]; Pedra Azul, XI.1970, 2 workers, F. M. OLIVEIRA [MZSP]; same locality, 800 m, XI.1972, 1 worker, SEABRA & ALVARENGA [MZSP]; Juiz de Fora, VII.1975, 6 workers, G. S. ANDRADE [MZSP]; Piracicaba, 2 workers [NHMB]; Teófilo Otoni, V.1925, 2 workers, FONSECA [MZSP]; same locality, 1928, 1 worker, ZEIDLER [MZSP]; Calado, Rio Doce, 12–15.II.1939, 1 male, MARTINS [MZSP]; Lassance, 20–31.I.1939, 1 worker, MARTINS LOPES & MANGABEIRA [MZSP]; Lagoa Formosa, Cabeceiras, 24–25.X.1954, 2 workers, Exp. Dep. Zool. [MZSP]; S. Caraça, Engenho, 800 m, XI.1961, 4 workers, KLOSS, LENKO, MARTINS & SILVA [MZSP]; Governador Valadares, 13–14.I.1958, 3 workers, K. LENKO [MZSP]; Arassuaí, 1926–27, 5 workers, 1 gyne, THIEMAN [MZSP]; Barro Alto, Nov. 1931, 5 workers [MCZC]. Espírito Santo: no further locality, 1 worker, JHERING [MHNG], XII.1906, 7 workers, 1 male, E. GARBE [MZSP]; S. Teresa, 2 workers, O. CONDE [MZSP]; Pt. Cachoeira, IV.1912, 6 workers, E. GARBE [MZSP]; Vitória, Penha, I.1957, 1 worker, R. MÜLLER [MZSP]; Linhares, IX.1972, 6 workers, M. ALVARENGA [MZSP]; Linhares, Dep. San. Veg., 1 male [MZSP]; Linhares, Parque Sooretama, 17–27.X.1962, 10 workers, 1 male, F. S. PEREIRA [MZSP]; same locality, 31.VIII.1962, 1 worker, H. REICHARDT [MZSP]; Pedro Canário, Conc. da Barra, X.1972, 6 workers, M. ALVARENGA [MZSP]. Mato Grosso: no further locality, 6 workers, GERMAIN [MCSN]; Highway BR. 174, km 198, 04.X.1984, 1 worker, J. ELIAS [INPA]; Reserva Humboldt 10°11' S, 59°48' W, 13–19.VII.1977, 1 gyne, B. C. RATCLIFFE [INPA]; Poconé, XI.1948, 1 gyne, VALETTE [MZSP]; Barra dos Bugres, Reserva Ecológica Serra das Araras, 16–29.I.1986, 17 workers, M. ZANUTO [MPEG]; Urucuru, 3 workers (syntypes of the stirps *crassispina*), SILVESTRI [NHMB]; Rio Aripuaña e Juruena, 10.1967, 2 workers, C. AMANN [MZSP]; Corumbá, 22.XI.1960, 4 workers, K. LENKO [MZSP]; Fazenda Santa Blanca, Corumbá, 08.XII.1960, 3 workers, K. LENKO [MZSP]; Serra do Urucum, Corumbá, 24.XI.1960, 14 workers, K. LENKO [MZSP]; Sinop , 55° 37' W, 12° 31' S, X.1974, 12 workers, M. ALVARENGA [MZSP]; Utiariti, Rio Papagaio, 26–29.X.1966, 5 workers, LENKO & PEREIRA [MZSP]; Sta. Terezinha, 30 km N of Barra Tapirapés, 05–10.II.1964, 2 workers, B. MALKIN [MZSP]; Carapó, 25.II.1969, 14 workers, G. R. KLOSS [MZSP]; Pimentel Barbosa, Rio das Mortes, XI.1949, 1 workers, DENTE & WERNER [MZSP]; Mato Grosso, 28.VII.1972, 12 workers, R. N. WILLIAMS [MZSP]; same locality, 7 workers, PONCE [MZSP]; same locality, XI.1961, 17 workers, F. M. OLIVEIRA [MZSP]; Barra do Tapirapé, 01.VIII.1962, 20.XI.1964, 9 workers, 1 male,

B. MALKIN [MZSP]; Rio Sacre, 28.VII.1961, 1 worker, K. LENKO [MZSP]; Fazenda Murtinho, XII.1929, 2 workers, R. SPITZ [MZSP]; Porto Murtinho, 19.XI.1929, 2 workers [MZSP]; Ilha do Taimã, R. Paraguai, 7.VIII.1980, 13 workers, C. R. F. BRANDÃO [MZSP]; Buriti, 21.VI.1972, 4 workers, 1 gyne, R. N. WILLIAMS [MZSP]; Fazenda Buriti, Chapada dos Guimarães, 09–14.II.1986, 1 worker, C. R. F. BRANDÃO & F. H. CAETANO [MZSP]; same locality, 1.1960, 3 workers, C. AMANN [MZSP]; same locality, 21.V.1972, 2 workers, R. N. WILLIAMS [MZSP]; same locality, X.1972, 1 worker, G. R. KLOSS & F. VAL [MZSP]; same locality, 14–22.XI.1982, 7 workers, M. ZANUTO [MPEG]; Cáceres, 15–18.X.1961, 3 workers, F. M. OLIVEIRA [MZSP]; same locality, 02.XII.1955, 1 male, M. ALVARENGA [MZSP]; S. Luiz de Cáceres, 1917, 2 workers, GARBE [MZSP]; Nioaque, 25.VII.1971, 5 workers, R. TRAVASSOS [MZSP]; Jardim, I.1962, 1 worker, Frei R. MUELLER [MZSP]; Fazenda Canaã, Três Lagoas, V.1967, 22 workers, F. LANE [MZSP]; Três Lagoas, left side of the Rio Sucuriu, XI.1966, IV.1967, 2 workers, F. LANE [MZSP]; Vila Vera, XI.1973, 8 workers, M. ALVARENGA [MZSP]; Xingu, XI.1961, 3 workers, ALVARENGA & WERNER [MZSP]; Taquerezinho, Coxim, 10–20.X.1963, 1 worker, V. C. A. CUNHA [MZSP]; Barra do Garça, 25.VII.1976, 3 workers, A. NEGRETT [MZSP]. B a h i a : without further data, 1 worker, P. SILVA [MZSP]; Maracás, Fazenda M. Inácia, Mata Cipó, 24–29.XI.1990, 18 workers, C. R. F. BRANDÃO, J. M. DINIZ, P. S. OLIVEIRA [MZSP]; Andaraí, Mata Carrasco, 13–14.XII.1990, 2 workers, C. R. F. BRANDÃO, J. M. DINIZ, P. S. OLIVEIRA [MZSP]; Ilhéus, IV.1919, 2 gynes, E. GARBE [MZSP]; Ilhéus, CEPEC, 6.VII.1993, 1 worker, 1 gyne, 1 male, J. H. C. DELABIE [CPCC]. G o i á s : Formosa, Lagoa Feia, 11.I.1973, 3 workers, W. W. KEMPF [MZSP]; Campinas, 1 worker, 1 gyne, SCHWARZMEIER [MZSP]; Itumbiara, 20.XI.1961, 1 worker [MZSP]; Rio de Coco, XI.1975, 3 workers, R. NEGRETT [MZSP]; Sta. Rita de Paraná íba, 10.VIII.1926, 2 workers, SCHWARZMEIER [MZSP]; Corumbá, Fazenda Manjolinho, VIII.1912, 6 workers, F. LANE [MZSP]; Jataí, Fazenda Cachoeirinha, 28.X.1962, 2 workers, Exp. Dep. Zool. [MZSP]; Gama, 19.II.1964, 4 workers, CARTER [MZSP]; 30 km N. Gurupi, 30.V.1966, 1 worker [MZSP]; Goiatuba, 21.XI.1960, 8 workers [MZSP]; Alto Paraiso, Encosta "Ferro de Encomar", 01–07.VII.1991, 1 worker, C. R. F. BRANDÃO, M. F. FRANÇOSO, A. A. REIS [MZSP]; Encruzilhada, 960–980 m, XI.1972 & 1974, 4 workers, SEABRA & ALVARENGA [MZSP]; Área de Zoologia, km 22, Ilhéus, Itabuna, X.1986, 2 workers, J. H. C. DELABIE [MZSP]; Ilhéus, VI.1919, 15 workers, 2 gynes, E. GARBE [MZSP, NHMB]; Água Preta, 28.VII.1943, 1 male, P. SILVA [MZSP]. M a t o G r o s s o d o S u l : Urucum, 2 workers, SILVESTRI [MCZC]. R i o d e J a n e i r o : no further locality, 10 workers, 1 gyne [MCSN, MHNG, ZSMC]; no further locality, 26.IX.1891, 13 workers [ZSMC]; no further locality, 1 worker, P. GERMAIN [MCSN]; no further locality, many workers, 1 gyne, EIDMANN [NHMB]; Petrópolis, 2 workers, T. BARBOUR [MCZC]; Barra do Piraí, 6 workers, Thayer Exp. [MCZC]; Itatiaia, 700 m, 09.XII.1947, 2 males, J. K. ZIKAN [MZSP]; Casca Dura, 07.XII.1905, 3 workers, M. WACKET [MZSP]; Petrópolis, X.1944, 2 workers, W. W. KEMPF [MZSP]; Pau da Fome, 01.IX.1940, 1 worker, LOPES & H. A. TRAV. [MZSP]; Porto de Caxias, III.1925, 3 workers, O. CONDE [MZSP]; Represa Rio Grande, VIII.1967, 2 workers, F. M. OLIVEIRA [MZSP]; same locality, IV.1966 & IV.1972, 4 workers, M. ALVARENGA [MZSP]; Represa Rio Grande, Guanabara, 13–15.X.1960, 6 workers (with red gaster!) & XII.1960, 2 workers (with normal gaster), 1 gyne, F. M. OLIVEIRA [MZSP]; Mendes, 09.X.1933, 5 workers, H. EIDMANN [NHMB]; same locality, 28.X.1933, 86 workers, several larvae and pupae, H. EIDMANN [NHMB]; Silva Jardim, VIII.1974, 2 workers, F. M. OLIVEIRA [MZSP]; Niterói, X.1928, 1 worker, BORGMEIER [MZSP]; Corcovado, X.1958, 1 gyne, ALVARENGA & SEABRA [MZSP]; same locality, 10.XI.1958, 1 gyne, 2 males, SEABRA & ALVARENGA [MZSP]. S ã o P a u l o : Caiuá, Fazenda Sta. Lucília, 03.I.1971, 1 worker, C. LANDIN [MZSP]; Piracicaba, Natal Velho, 22.IV.1968, 1 worker [MZSP]; Salto Grande, II.1911, 1 worker, H. LÜDERWALDT [MZSP]; Pirapora, 1912, 2 workers, GARBE [MZSP]; Itápolis, II.1960, 2 workers, B. SCHWEITZER [MZSP]; Juquiá, XI.1929, 1 worker, J. LANE [MZSP]; Anhembi, 01.III.1960, 2 workers, L. TRAVASSOS [MZSP]; Barra de Una, S. Sebastião, 03.VII.1961, 2 workers, 1 male, K. LENKO [MZSP]; Praia do Itagaré, Santos, 10.X, 28.XI.1961, 2 workers, RABELLO [MZSP]; Franca, I.1911, 2 workers, E. GARBE [MZSP]; Fazenda Itaquerê, Boa Esperança do Sul, 22–28.XI.1963, 8 workers, K. LENKO [MZSP]; Fazenda Campininha, Mogi Guaçu, 04.IV,

07.V.1977, 2 workers [MZSP]; Monte Alto, Jaboticabal, VIII.1914, 3 workers, R. v. IHERING [MZSP]; Praia Massaguaçú, Caraguatatuba, 28–30.V.1962, 2 workers, Exp. Dep. Zool. [MZSP]; S. Paulo capital, XII.1929, 1 worker [MZSP]; Onda Verde, Fazenda S. João, I.1946, 2 workers, F. LANE [MZSP]; Cachoeira das Emas, Mogi Guaçu, 15.II.1965, 6 workers, R. G. KLOSS [MZSP]; Raiz da Serra, 27.IX.1907, 1 worker, H. LUEDERWALDT [MZSP]; Agudos, 18–19.IX.1953, 7 workers, C. GILBERT [MZSP]; same locality, 10.X.1952, 1 gyne, W. W. KEMPF [MZSP]; same locality, 03.XI.1955, 1 male, W. W. KEMPF [MZSP]; Itanhaém, 30.XII.1977, 18 workers, L. R. FONTES [MZSP]; Cajuru, Fazenda Santa Carlota, 21° 17' S, 47° 18' W, 1 worker, R. SILVESTRI [MZSP]. Paraná: Rondon, 1 worker [MZSP]; Rio Paraguay, 2 workers, K. FIEBRIG [MCZC].

Bolivia: no further locality, 4 workers, BALZAN [MCSN]; Dto. Carijó, Pcia. Gran Villa Moules, 9 workers, A. MARTÍNEZ [MZSP]; Chiquitos, 1 gyne, STAUDINGER [MCSN]; Songo, 1 male [MCSN]. Beni: Lago Rogagua, Rosario, 3 workers, W. M. MANN [MZSP]; Rurrenabaque, 3 workers, W. M. MANN [MZSP]; Río Beni, Salinas, 1891, 4 wokers, BALZAN [MCSN]; El Beni, NE San Borja, Palm camp, savannah, 25–30.VII.1988, 10 workers, R. W. BROOKY [USNM]. La Paz: Coroico, 1 worker [MCZC]. Santa Cruz: Yacapani, 10.VIII.1965, 2 workers, J. D. CANDIA [MCZC]; Puerto Suárez, Cerrito, 2 workers, WITTMER [MZSP]; Sara, Nueva Moka, II.1950, 6 workers, A. MARTÍNEZ [MZSP]. Cochabamba: no further locality, II.1953, 2 workers, A. MARTÍNEZ [MZSP].

Argentina: Formosa: no further locality, 5 workers [MCSN]; no further locality, 3 workers (syntypes of the stirps *crassispina*), JOERGENSEN [NHMB]; Laishi, 2 workers, ZURFLUH [NHMB]. Misiones: without further locality, III.1960, 1 worker, DELAPIERRE [NHMB]; idem, 1 worker [MHNG]; Loreto, 14.VIII.1949, 1 male, N. KUSNEZOV [MCZC]; same locality, 2 males, N. KUSNEZOV [MHNG].

Paraguay: no further data, 1 gyne [MCSN], idem, 1 worker (syntype of the stirps *crassispina*) [NHMB], 1 worker [MZSP]. La Cordillera: San Bernardino, 3 workers, K. FIEBRIG [NHMB]. Caaguazú: Between Caaguazú and Cel Oviedo, 17.I.1970, 1 worker, W. W. KEMPF [MZSP]. Alto Paraná: Pastoreo, 18–20.IX.1974, 12 workers, P. DUELLI [MZSP]; Assunción: S. Bernardino, 3 workers, [ZSMC]; S. Bernardino, 2 workers, 2 gynes, 1 male, FIEBRIG [MHNG].

Discussion. - This species is the largest and one of the commonest of the genus. The mature colonies are composed of several thousands of individuals which, while foraging, can almost cover some tree trunks even in urban areas. This explains the long synonymic record. KEMPF (1951) gives a very exhaustive account of the variability and proposed five new synonyms, mostly among the plethora of infraspecific names proposed by SANTSCHI. Curiously enough, KEMPF (l. c.) retained SANTSCHI's variety *erecta* (an unavailable name of which he did not see the types) and raised it to subspecific rank. This decision was based largely on a single character, the sculpturation of the first gastral tergite which should show a morphoclinal tendency to increase from North to South: *erectus* (the northern race) should reach Colombia to the South, and the rest of the range should be occupied by *atratus* s. str. Examination of two Panamanian syntype workers of the var. *erecta* in NHMB scarcely permits to distinguish them from other specimens of Brazilian provenance. In the same paper KEMPF (1951: 119) noticed the incongruence of a Honduran specimen available to him and belonging to the hypothetical southern form. It appears, hence, that there are no sufficient reasons to maintain the name *erectus* even at infraspecific level. To the discussion on the individual and geographic variability already given by KEMPF (1951), we add only the presence of individual workers and nest series with red gaster (var. *rufiventris* EMERY) occurring sympatrically with the black form and apparently without transition to it as already listed under the material examined. The fact that this

colour morph is to be found in both sister species, *atratus* and *marginatus*, emphasises its lack of taxonomic status. The specimens with reddish gaster may be freshly moulted individuals.

The photograph presented by SEAR (1996) under the name *Zacryptocerus* spp. must be referred to this species or to the closely related *marginatus*.

FERNÁNDEZ et al. (1996) report this species also from the Colombian states of Arauca, Boyacá, Meta, Santander, Vichada and Caquetá.

Distribution: Belize?, St. Thomas Island?, Virgin Islands? (FOREL, 1901 c), Costa Rica, Panama, Colombia, Ecuador, Peru, Trinidad, Venezuela, Guyanas, Brazil, Bolivia, Argentina, Paraguay, Uruguay.

Cephalotes marginatus (FABRICIUS) new combination, bona species

Fig. 41

Cryptocerus marginatus FABRICIUS, 1804: 419. Gyne. Original description. Type locality: "in America meridionali", actually Essequibo (Guyana). Type material: Holotype winged gyne (wings detached) labelled "Essequibo, Smidt, Mus. J. Lund, *Cryptocerus atratus* (Fabr.) Linn., *marginatus* Fabr.", in ZMUC, examined.

Cryptocerus atratus (LINNAEUS), KLUG, 1824: 200. Nec LINNAEUS, 1758.

Cephalotes decemspinosus SANTSCHI, 1920: 148. Worker. Original description. Type locality: St. Jean du Maroni (French Guyana). Type material: 4 syntype workers from St. Jean du Maroni, French Guyana, Le Moult in NHMB (examined), lectotype worker, in Coll. Borgmeier (MZSP), designated by KEMPF, 1951 same data as the syntypes. New synonym.

Cephalotes decemspinosus var. *spissus* (sic) SANTSCHI, 1929: 302. Worker. Original description. Type locality: surroundings of the Lucie River (Surinam). Type material: 3 syntype workers labelled Suriname-Exped., Lucie-riv. -Gebied, VII-VIII. 1926, NHMB, examined. Synonymy with *decemspinosus* by KEMPF, 1951: 125.

Cephalotes decemspinosus SANTSCHI, KEMPF, 1951: 125.

Cephalotes decemspinosus SANTSCHI, FERNÁNDEZ et al., 1996: 378.

Diagnosis. - A member of the *atratus* clade exhibiting, in the worker and gyne, the following characters separating it from the sister species *atratus*: abundant suberect pilosity on the ventral face of the gaster and – in the workers – median pronotal spines ca. 1/4 of the size of the external ones instead of simply minute or absent as in *atratus*. The males of the two species differ in the CI values as given under the respective descriptions.

Worker. - Moderately variable in size. Head with the sides (frontal carinae) subparallel, very weakly crenulate only on the anterior fourth and upturned laterally. Vertexal border continuing the frontal carinae and sloping ventrally, bearing two pairs of lateral spines, the distal pair ca. 1/2 longer than the proximal one, very weakly carinate to straight posteriorly. Eyes ca. at 6/7 of head length posteriorly and protruding from the ventral border of the antennal scrobes.

Mesosoma relatively slender. Pronotum making an angle of ca. 90° with the mesonotum, straight and inclined antero-ventrally at about 45° on the longitudinal body axis. Posterior pronotal third with two pairs of spines, the external pair almost continuing laterally the pronotal surface and long as half of the maximum head width; the median pair, perpendicular to the pronotum, is regularly much longer than in *atratus*, ca. 1/4 as long as the external pair. Promesonotal suture well marked. Mesonotum straight and flat in profile. Propodeal suture deeply impressed. Propodeum with basal and declivous faces subequal in length and forming an angle of ca. 90°. Basal face practically flat, passing into the sides with a round angle. Declivous face very weakly concave. Propodeal spines only slightly shorter than the external pronotal ones, obliquely pointing backwards. Metapleural-propodeal suture oblique and deeply impressed laterally.

Petiole with slightly concave anterior and slightly convex posterior faces, bearing two small, dorso-lateral denticles. Postpetiole subequal to petiole in width, narrower posteriorly,

with a very short, perpendicular anterior face and nearly flat dorsal one; the angle between the anterior and superior faces bears a pair of short spines, slightly longer than the petiolar ones and directed upwards; ventrally, another pair of spines obliquely directed forwards, subequal to the dorsal ones in length but thinner.

Gaster elongate, incised at the articulation with the postpetiole and marginate anteriorly.

Mid and hind tibiae strongly compressed laterally and with marginate external borders.

Pilosity and sculpture. Whole body, except the spines and the appendages covered by dense, superficial, oval pits. The pits on the head, mesosoma and pedicel bear a thick, truncate hair and can be interpreted as sensilla auricillica. The pits on the gaster are more superficial, each pit bearing simply pointed hairs (in *atratus* the deeper pits are generally limited to the head and pronotum). A few suberect, thick bristles on the anterior pair of vertexal spines, on both pairs of pronotal spines and on the pedicel. Numerous yellowish standing hairs on the posterior border of all gastral segments and at least on the distal half of the first gastral sternite. Legs with few, yellowish, subdecumbent or decumbent hairs, particularly on the coxae and on the tibiae.

Colour black moderately shining except the frontal carinae, ferrugineous.

Measurements (in mm) and indices: TL 9.60–17.00; HL 2.04–3.50; HW 2.60–5.20; EL 0.53–0.80; PW 2.60–5.00; PeW 0.68–1.08; PpW 0.75–1.28; HBaL 1.60–2.48; HBaW 0.38–0.60; CI 127.1–148.6; PI 88.2–110.6; PPeI 382.3 –555.5; PPpI 346.7–510.2; HBaI 23.6–24.8.

G y n e . - Head slightly wider than long, with the sides converging anteriorly and weakly crenulate only on their anterior fifth. Clypeus broadly concave. Vertexal border weakly concave, nearly straight. Abroad median dorsal depression of the head capsule at about 2/3 of its length. Frontal line reaching the median depression or continuing through it up to the median ocellus. Two pairs of lateral vertical spines subequal in size and disposed perpendicularly to the vertexal angles; a third pair of smaller, blunt, vertexal spines behind and between the pair ocelli. Eyes, in dorsal view, not covered by the frontal carinae. Ocelli deeply impressed and subequal in distance each one to the other two. Mandibles robust, serially toothed and transversely impressed at mid length. Antennal scape thick; funicular joints gradually increasing in size from the second to the last.

Mesosoma, in dorsal view, remarkably broadened at the height of the mesopleurae, with flat mesonotum and scutellum, both higher than the pronotum and propodeum in profile. Humeral spines developed and pointing perpendicularly to the major body axis, followed by a pair of minute denticles caudally. Medial pronotal spines much broader and shorter, obtuse to pointed. Propodeum with basal face gently sloping backwards, shorter than the declivous face, which is nearly straight. Propodeal spines robust, their dorsal surface complanary with the basal face of the propodeum, long 1/2 of their distance at the apex, diverging caudally.

Petiole sessile, slightly lower than the postpetiole, with anterior face flat and posterior face only slightly shorter than the anterior one, bearing only two weak dorsal protuberances and no spines. Postpetiole slightly broader than petiole, twice broader than long, bearing two more prominent dorsal protuberances and a broad ventral lamella.

Gaster incised at the articulation with the postpetiole, not marginate; in dorsal view only the first and part of the second tergites visible.

Legs with mid and hind tibiae compressed laterally and distally marginate on the external face.

Fore wings infuscate with very dark *R+ Sc* connected with a marked pterostigma. *Rsf5* connected with *R1*. *R1* almost reaching or entirely reaching and outlining the wing border. *A*, *Cu-A*, *Cu-A1* and *Mf4* well marked and nearly reaching the wing border. Hind wings with well marked *R*, *M+CuA*, *1A*, *CuA*, *r-m* and *M*. Distal parts of *1A*, *CuA* and *M* obsolete and nearly reaching the wing border.

Sculpture and pilosity as in the worker but more uniform over the whole body, with the pits more deeply impressed on the pedicel. Abundant, short, truncate, yellowish hairs on the terminal parts of the gastral segments and at least on the distal half of the first gastral sternite.

Colour uniformly black, more shining on the gaster, with a ferrugineous strip parallel to the frontal carinae where the integument is thinner and semi-transparent.

Measurements (in mm) and indices: TL 19.60–20.30; HL 3.28–3.70; HW 4.35–4.90; EL 0.83–0.88; PW 4.60–4.90; PeW 1.44–1.72; PpW 1.60–1.64; HBaL 2.00–2.20; HBaW 0.60–0.61; CI 127.0–132.6; PI 89.8–97.9; PPeI 315.8–331.1; PPpI 287.5–306.2; HBaI 27.3–30.5.

M a l e (previously undescribed). - Head much broader than long, with the cheeks strongly converging anteriorly. Vertexal margin prolonging backwards into a neck. Vertexal angles diverging towards the posterior border of the eyes, with a median pair of obtuse, triangular denticles sometimes connected through a carina to the external pair denticles close to the eyes. Frontal carinae more or less raised over the head dorsum. Frontal line marked and reaching the median ocellus posteriorly. Clypeus moderately convex anteriorly and remarkably raised in the middle, its medial part much higher than the mandibular plane. Eyes strongly protruding on the sides of the head which is much narrower in front than behind the eyes. Ocelli delimiting a subtriangular area adjecting dorsally over the already prominent frontal area. Antennal scape thick, ca. two times longer than broad and three times longer than the first funicular joint; second funicular joint ca. 1.5 times longer than the scape; third funicular joint slightly shorter; remaining antennomeres thickening from the base to the apex. Mandibles elongate and weakly carinate laterally.

Mesosoma elongate, in dorsal view the sides continuously arched from the anterior pronotal border to the propodeum. Pronotal sides diverging backwards, sometimes with a pair of minute denticles. Mayrian furrows deeply impressed. Mesonotum and scutellum gently convex in sides view. Propodeum with basal and declivous faces making an angle of ca. 100° and separate by a ridge bearing, at its sides, two small teeth. Petiole and postpetiole subequal in length and width, with their maximum width anteriorly. Petiolar node subrectangular; its anterior face truncate and laterally delimited by a pair of denticles. Postpetiole subexagonal. Gaster elongate; its maximum width subequal to the maximum width of the thorax.

Genitalia and subgenital plate as in Fig. 41.

Sculpture. Head punctate and covered by irregular foveae and short rugosities; the foveae and the rugosities broader on the posterior part of the head dorsum and on the whole ventral part of the head. Mesosoma punctate and densely covered by foveae more regular than those on the ventral part of the head. Anterior half of the basal face of the propodeum with the same type of sculpture as on the posterior part of the head dorsum; posterior half of the basal face and anterior part of the declivous face with longitudinal rugosities, the rugosities transversal on the posterior part of the declivous face. Pleurae punctate and with longitudinal rugosities on the pro- and lower metapleurae, the rugosities thicker on the lower metapleurae. Meso- and upper metapleurae covered by irregular foveae, sparser on the upper mesopleurae. Pedicel punctate and with very thin, irregular, longitudinal rugosities more impressed on the sides. First gastral tergite reticulate; remaining tergites and sternites superficially reticulate and shining. Legs punctate; the punctures more impressed on the tibiae.

Pilosity. Head and mesosoma covered by long, thick, pointed, erect, golden hairs. The same hairs, but rarer, on the sides of the petiole and postpetiole. Gaster, dorsally, only with few short hairs at the end of each segment, practically bald; ventrally, numerous, long, golden hairs as in the worker and in the gyne. Antennae only pubescent. Legs with similar but shorter and appressed, golden hairs.

Colour. Head, mesosoma, petiole and postpetiole, coxae and trochanters black. Gaster and remaining parts of the legs yellowish-brown; antennae brown and opaque.

Measurements (in mm) and indices: TL 11.34–13.88; HL 1.64–1.76; HW 1.80–2.16; EL 0.62–0.72; PW 1.72–2.16; PeW 0.84–0.96; PpW 0.98–1.08; HBaL 1.80–2.08; HBaW 0.25–0.30; CI 109.7–122.7; PI 98.1–104.6; PPeI 179.2–257.1; PPpI 172.0–204.1; HBaI 11.5–15.9.

M a t e r i a l e x a m i n e d. - **Guyana**: Essequibo: 1 gyne (holotype), SMIDT [ZMUC].

Surinam: Surroundings of the Lucie River, 3 workers (syntypes of the var. *spissa*) [NHMB].

French Guyana: St. Jean du Maroni, 5 workers (syntypes of *decemspinosus*), 1 gyne, LE MOULT, [4 syntypes NHMB, 1 MZSP]; St. Laurent du Maroni, 1 gyne, LE MOULT [NHMB]; Nouveau Chantier, 2 workers, 1 gyne, LE MOULT [NHMB, MHNG]; Maroni, 1 male [MCZC]; Forêt de Balaté, St. Jean du Maroni, 16.10.1969, 1 worker, BALCHOWSKY & GRUNER [MZSP].

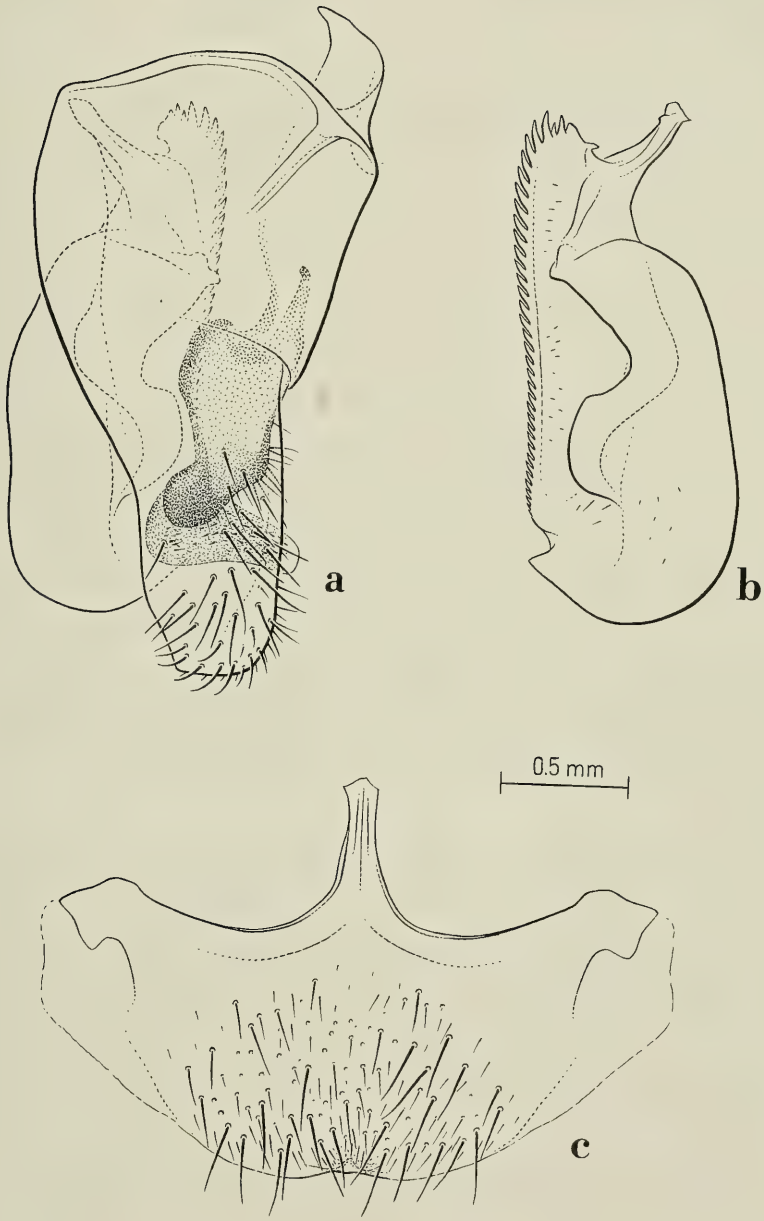


Fig. 41. *Cephalotes marginatus* (FABRICIUS). Male from St. Laurent du Maroni, French Guyana. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Colombia: A n t i o q u i a : Nare, 1 worker, 1 male [ZSMC]. A m a z o n a s : La Chorrera, 50 km downhill Plateau de Grés, Adofiki, 06–10.X.1073, 3 workers, J. DESPLATS [MNHN]; La Chorrera, 30 km downhill Río Igara Paraná , 20–24.II.1974, 3 workers, J. DESPLATS [MNHN].

Brazil: A m á p á : Serra do Navio, 10.VII.1980, 1 worker, P. TADEO [MPEG]; Paredão, 6.V.1979, 8 workers, W. L. OVERAL [MPEG]; Mazagão, Fazendinha, 9.XI.1978, 3 workers, W. FRANÇA [MPEG]; Santana, Rio Amazonas, 14.VI.1966, 1 gyne, W. WEYRAUCH [MZSP]. A m a z o n a s : no further locality, 01.IV.1976, 1 gyne, I. S. GORAVEB [INPA]; no further locality, 2 workers, 1 male, H. W. BATES S. [ZSMC]; Manaus, estrada do Aleixo, km 11, 14.II.1976, 1 gyne, I. S. GORAVEB [INPA]; Manaus, Est. Itacoatiara, 23.VIII.1961, 1 gyne, MOZORTH [INPA]; Manaus, 12.IV.1982, 1 gyne, E. L. OLIVEIRA [INPA]; Manaus, INPA Campus, 12.XII.1980, 2 workers, C. N. ARCANJO [MPEG]; Médio Purus, 21.VII.1979, 1 gyne, J. & S. CAMPBELL [INPA]; Rio Unini, Lago Pedras, left side, 22.XI.1995, 23 workers, BINDA & ALENCAR [INPA]; Reserva Ducke, 6.III.1960, 1 gyne, P. N. MELLO & A. FAUSTINO [INPA]; same locality, 19.I.1982, 1 worker, ADIS et al. [INPA]; same locality, 22–26.I.1996, 2 gynes, 1 male, M. L. DE ANDRADE [INPA]; same locality, 10.III.1988, 1 gyne, A. C. FERREIRA et al. [INPA]; same locality, V.1968, 1 gyne, FAUSTINO [INPA]. Tarumã-Mirim, 19.I.1976, 1 gyne, J. ADIS [INPA]; Reserva INPA, II.1976, 1 gyne, V. P. DANIEL & L. REPP [MZSP]. P a r á : no further locality, 1 gyne [USNM]; Belém, II.1957, 1 gyne, PEREIRA & MACHADO [MZSP]; Belém, Ariramba, 20.VII.1983, 1 worker, M. C. BARROS [MPEG]; Belém, Mocambo, different dates and collectors, 3 workers [MPEG]; Serra Norte, 3 Alfa, 26.VI.1985, 1 worker, M. Zanuto [MPEG]; Tucuruí, right side, 16.III.1979, 9 workers, R. B. NETO [MPEG]; Acará, 7.XII.1977, 2 workers, W. L. OVERAL [MPEG]; S. C. Odivelas, 27.V.1978, 1 gyne, P. TADEO [MPEG]; Abaetuba, 9.VI.1979, 26 workers, M. F. TORRES & O. UCHÔA [MPEG]; Castanhal, 12.IX.1984, 1 worker, M. F. TORRES [MPEG]; Vizeu, 27.V.1978, 1 worker, F. F. RAMOS [MPEG]; Vizeu-Inaicuara, 26.V.1988, 6 workers, J. DIAS [MPEG]; Itaituba, Parque Nacional da Amazônia, 12.XI.1978, 1 worker, W. L. OVERAL [MPEG]; Monte Dourado, 11.VII.1979, 1 worker, N. VIANA [MPEG]; Benevides, Fazenda Morelândia, 5.II.1981, 1 gyne [MPEG]; Óbidos, lower Amazonas, 18.IV.1960, 1 gyne, DIRINGS [MZSP]; Rio Trombetas, 4.X.1985, 1 gyne, COMANDER [INPA]. M a r a n h ã o : Imperatriz, Ribeirãozinho, 2–5.VIII.1989, 2 workers, F. F. RAMOS [MPEG].

D i s c u s s i o n . - The Fabrician type of *marginatus* (a winged gyne from Guyana) is geographically close to *decemspinosus* (from French Guyana) and does not differ in any significant way from specimens of the previously undescribed gyne of the latter in NHMB. KEMPF (1951) was rather sceptical of the specific value of *decemspinosus* of which he saw only one undoubted specimen and a few doubtful Colombian and Brazilian representatives. He separated *decemspinosus* from *atratus* basically on the pilosity under the gaster, the thicker foveae on the pronotum and mesonotum, and the much longer median propodeal spines. The microsculpture of the pronotum and mesonotum may be more difficult to appreciate in some specimens, but, among the material available to us, the longer median pronotal spines appear to characterise this species rather well, except for one syntype of the var. *spissa*. But the character constant within all the specimens we examined is the abundant ventral pilosity of the gaster. This difference is consistent also for the few gynes of the two species we examined. We share, in part, the worries of KEMPF about the specific status of this taxon, but it must be added that, if the material of *marginatus* available to us is not very copious, we have abundant evidence of the lack of ventral gastral hairs among the very rich *atratus* material we have been able to see. In addition, the two species are closely sympatric at least in French Guyana.

The CI appears to separate well the males of the two species and may be useful also to differentiate the gynes as it appears from the following comparison:

CI	worker	gyne	male
atratus	130.0–136.4	120.0–126.5	128.3–131.9
marginatus	127.1–148.6	127.0–132.6	109.7–122.7

KEMPF (1951) tentatively synonymised SANTSCHI's *decemspinosus* var. *spissa* with the nominal form without having actually seen it. Examination of the type material of both taxa confirms entirely KEMPF's intuition.

FERNÁNDEZ et al. (1996) report this species generically from the "Norte de Colombia" which appears to represent the northernmost record for this species so far.

D i s t r i b u t i o n : Guyanas, Surinam, Colombia, Brazil.

Cephalotes alfaroi (EMERY) bona species
Figs. 42, 43

Cryptocerus Alfaroi EMERY, 1890: 76. Worker and soldier. Original description. Type locality: Alajuela (Costa Rica). Type material: two workers labelled "Alajuela, Alfaro" in MCSN; one worker and one soldier with syntype label only, in MHNG, examined.
Cryptocerus alfaroi EMERY, FOREL, 1899 a: 48, pl. 3, figs. 7 & 8. Worker and soldier.
Cephalotes alfaroi EMERY, EMERY, 1914 b: 39. First combination in *Cephalotes*.
Cephalotes alfaroi EMERY, KEMPF, 1951: 112, figs. 98, 99, 101, 102. Soldier.
Cephalotes serraticeps (SMITH), KEMPF, 1964 a: 437. Nec SMITH, 1858. Partim. Misidentification.
Cephalotes alfaroi EMERY, WHEELER & WHEELER, 1983: 607. Larva.

D i a g n o s i s . - A member of the *atratus* clade characterised by the crenulate frontal carinae bearing clavate hairs (less so than in the sister species *serraticeps*), and differing from its sister species *serraticeps* by the longitudinally rugulose head and for the narrower and not laterally compressed first tarsomeres of the mid and hind legs.

W o r k e r (Fig. 42) (description of KEMPF, 1951). - "Length 10.0 mm. Median head length 2.24 mm. Weber's length of thorax 3.17 mm. Similar to the major worker, from which it differs in the following features: Frontal carinae partly semi-transparent, fuscous-ferruginous, converging in front, lateral border straight, preatly upturned. Each occipital angle with a pair of triangular spines, the anterior spine with a minute tooth arising from the base, projecting outward. Occiput continuous with vertex , not truncated, the pair of teeth on vertex obsolete. Integument subopaque, more sharply punctured and finely longitudinally rugulose caudad. Thorax subopaque, longitudinally areolate-rugose above and laterally. Scapular spines more slender, longer, acuminate, median teeth small, their bases transvese in the form of a crest. Spines of petiole more conspicuous. Sculpture of gaster sharper and coarser, distinctly longitudinally rugulose."

Measurements (in mm) and indices: TL 8.40–11.46; HL 1.80–2.48; HW 2.20–2.88; EL 0.44–0.56; PW 1.76–2.70; PeW 0.47.0.62; PpW 0.60–0.80; HBaL 1.72–2.12; HBaW 0.35–0.47; CI 116.1–122.2; PI 106.7–125.0; PPeI 374.5–435.5; PPpI 280.0–360.0; HBaI 20.3–22.2.

S o l d i e r (Fig. 43) (description of KEMPF, 1951). - "Length 13 mm. Median head length 2.97 mm. Weber's length of thorax 4.15 mm. Black; the following dark ferruginous: tip of last funicular segment, apices of last tarsal segments, claws.

Head subfulgid, subquadrate, microscopically punctate, coarsely and sparsely foveolate. Mandibles reticulate-rugose, with a distinct apical and preapical tooth. Clypeur and frontal area vestigially set off. Frontal carinae crenulated, their sides moderately arcuate and slightly upturned. Vertex with a transversely located pair of blunt swellings. Occiput subtruncate mesad. Occipital angles with a rather large and obtuse posterior tooth, the anterior tooth scarcely

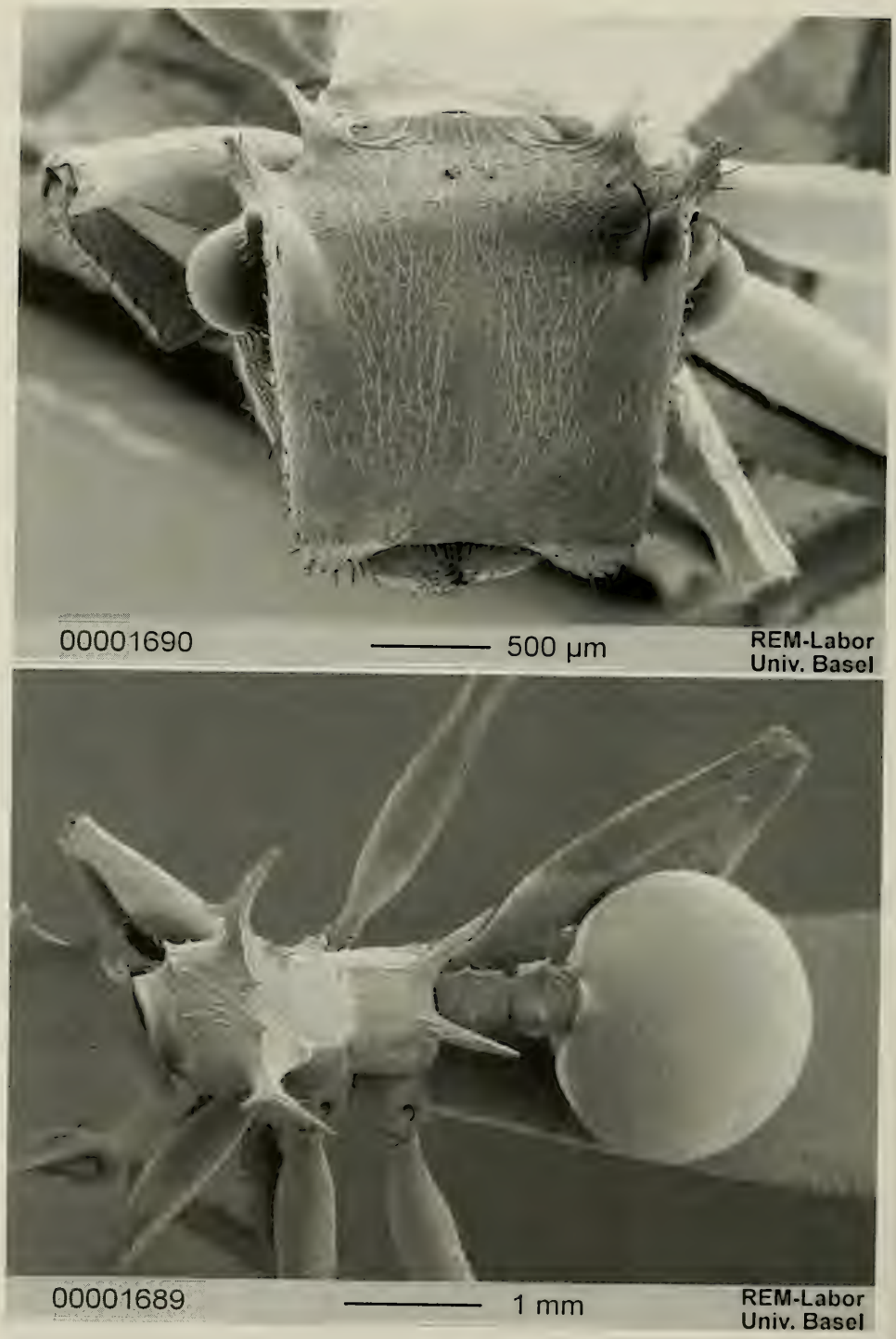


Fig. 42. *Cephalotes alfaroi* (EMERY). Worker from Zent, Limón, Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

distinct from the crenulated border of the frontal carinae. In lateral view three minute denticules project ventrad from the frontal carinae, in front of the eye. Eyes beneath the antennal scrobe. Maxillary palpi 5-segmented. A small but distinct tooth projecting from the sides of the head, somewhat above and behind the eyes. Scape incrassated distad, attenuate and subcylindrical proximad.

Thorax subopaque. Shoulders obtusely angulate. Dorsal face of pronotum inclined cephalad, with two stout, rather acute median spines and a lateral, stout, more or less apically truncate scapular spine on each side, above and behind the shoulder. A minute tooth projecting distad from the anterior side of the scapular spine. Promesonotal suture distinct. Mesonotum moderately inclined caudad, flat, marginate laterad, its posterior corners marked by somewhat raised, blunt swellings. Mesoepinotal suture distinctly impressed. Basal face of epinotum somewhat inclined cephalad; about as long as wide, its sides immarginate, subequal in length to the declivous face. Lower mesopleura with an anterior tooth. Epinotal spines longer than basal face, divergent, somewhat upturned, subacuminate. Integument microscopically and densely punctate, sparsely foveolate. Middle portion of femora moderately incrassate, the upper face strongly marginate on the distal end. Tibiae prismatic. Middle and hind basitarsus compressed and greatly flattened.

Petiole subopaque; subquadrate from above, its sides subparallel. Anterior face obliquely truncate. Anterior corner of dorsal face with a laterally projecting minute tooth. Integument finely and densely punctate, and sparsely foveolate. Postpetiole wider than long, with a pair of conspicuous recurved teeth above, on the anterior border. Ventral face with a distinctly ventrally projecting lobe. Sculpture as on petiole. Densely foveolate-rugose.

Gaster subfulgid. First tergite and firts sternite microscopically and very shallowly punctate, almost smooth, fulgid, except the narrow posterior margin, which, as also the exposed portion of the remaining tergites and sternites, are more sharply punctured and transversely rugulose.

Most of the foveolae contain a thin, short, decumbent seta. Margin of frontal carinae with a row of somewhat clubbed setae within the crenulations, along their entire length. Mandibles, lowe rsurface of head, spines of thorax, postpetiole appendages and gaster above and below, with sparse, erect setae."

Measurements (in mm) and indices: TL 12.62–13.02; HL 2.92–3.04; HW 3.52–3.60; EL 0.68; PW 3.20–3.32; PeW 0.74–0.84; PpW 0.87–0.92; HBaL 2.04–2.08; HBaW 0.52; CI 118.4–120.5; PI 106.0–112.5; PPeI 381.0–448.6; PPpI 347.8–381.6; HBaI 25.0–25.5.

Material examined. - **Costa Rica**: illegible name (Emery's handwriting), 1 worker (syntype?) [NHMB]; Alajuela, 3 workers, 1 soldier (syntypes), Alfaro [MCSN, MNHG]; Jiménez, 1895, 3 workers [MCSN]; Zent, Limón, 01.IX.1958, en cacao, 13 workers, 2 soldiers, F. Lara [MZSP, MCZC]; Ebene Limón, Hamburg Farm, Reventazón, 1 worker, 2 soldiers, Reichensperger [MZSP]; Parrita, Río Parrita, vicinity of Pacific Ocean, 02.VIII.1937, 1 worker, A. Alfaro [MZSP].

Panama: Bugaba, 800–1500 ft., 7 workers, 1 soldier, Champion [MHNG, MCZC].

Discussion. - Kempf (1964 a) examined the holotype gyne of *serraticeps* (a Brazilian and Peruvian endemic) in London and proposed its synonymy with the junior *alfaroi* (of which only the worker is known). It is probable that during his visit at the British Museum Kempf had no *alfaroi* material to compare with the type of Smith. All the *alfaroi* specimens we have seen (including the syntypes) differ from *serraticeps* by the minute longitudinal rugulation of the head and of the mesosoma (properly described by Kempf, 1951), by the less clavate hairs over the frontal carinae and by the shape of the tarsomeres of the fore, mid and hind legs, less compressed, narrower and longer than in *serraticeps*.

Distribution: Panama, Costa Rica.

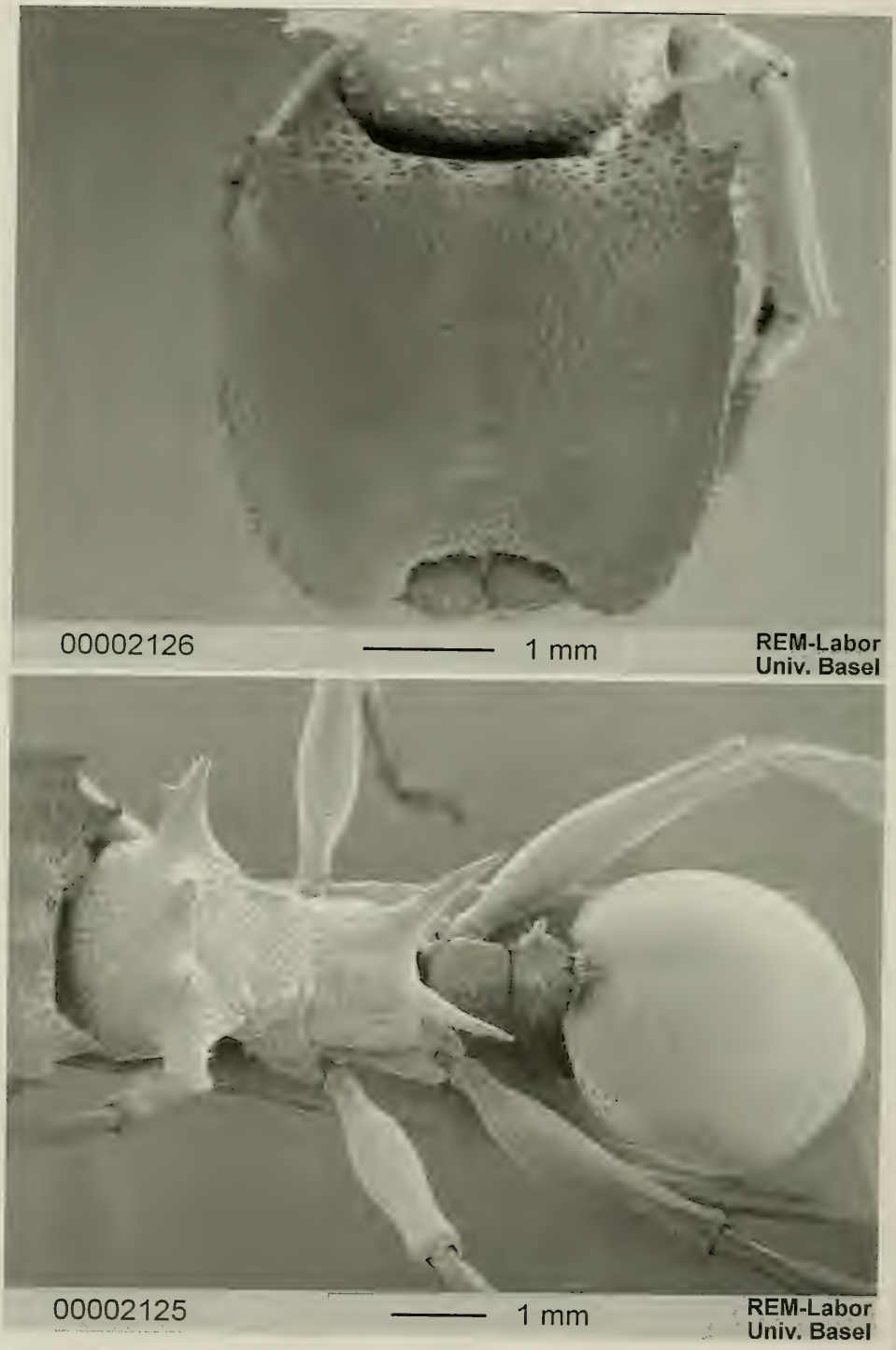


Fig. 43. *Cephalotes alfaroi* (EMERY). Soldier from Bugaba, Panama: head (top) and meso- and metasoma (bottom) in dorsal view.

Cephalotes serraticeps (SMITH)

Figs. 44, 45, 46, 47, 48

Cryptocerus serraticeps SMITH,1858:188. Gyne. Original description. Type locality: Ega (= Tefé), Amazonas (Brazil). Type material: Holotype gyne labelled "*Cryptocerus serraticeps*, Type Sm., 56 84" in BMNH (KEMPF, 1964 a: 437), examined.

Eucryptocerus serraticeps (SMITH), KEMPF, 1951: 132. First combination in *Eucryptocerus*.

Cephalotes serraticeps (SMITH), KEMPF, 1964 a: 437. First combination in *Cephalotes*.

Cephalotes alfaroi EMERY, KEMPF, 1964 a: 437. Nec EMERY, 1890. Misidentification.

D i a g n o s i s . - A member of the *atratus* clade characterised in the worker, soldier and gyne by the autapomorphic laterally compressed and distally much narrower first tarsomeres of the mid and hind legs; from the sister species *alfaroi*, in addition, it can be separated by the strongly crenulate frontal carinae.

W o r k e r (Figs. 44, 45) (previously undescribed). - Head subquadrate. Frontal carinae crenulate, diverging backwards, not covering the cheeks posteriorly and ending behind the eyes. Vertexal margin laterally carinate and medially prolonged backwards in a "neck"; vertexal angles with two pairs of spines, the internal pair narrower than the external one. Antennal scrobes over the eyes, surpassing their posterior border. Eyes globose. Postoccipital suture open antero-ventrally. Cheeks ventrally marginate. Mandibles massive and with a superficial tumulus.

Mesosoma flat and sloping posteriorly. Scapular angles anteriorly prominent. Humeral angles with a pair of long, thick spines directed upwards; tip of the pronotal spines bispinose, the anterior arm directed forwards, ca. half as long as the posterior one, directed backwards. Pronotal dorsum with a thick, transversal carina converging medially to a longitudinal, anterior one. Promesonotal suture impressed laterally only. Mesonotum unarmed, converging posteriorly. Propodeal suture impressed. Propodeum with differentiated basal and declivous faces and bearing a pair of thick, long, diverging spines directed upwards; declivous face straight and with little converging sides.

Petiole with differentiated anterior and superior faces; anterior face truncate; superior face angular in side view, with a pair of spines at the edge. Petiolar sides almost parallel and unarmed. Postpetiole broader and shorter than the petiole, slightly convex, its dorsum with a pair of pointed spines anteriorly. Postpetiolar sides convex anteriorly and converging posteriorly.

Gaster oval, with a pair of well developed anterolateral lamellae almost reaching the stigma but surpassing the latter in form of a thin carina only.

Mid and hind femora neither angulate nor denticulate; their dorsum with a pair of longitudinal carinae more impressed on their distal half. Mid and hind tibiae laterally compressed and with a pair of well impressed longitudinal carinae dorsally. Mid and hind (Fig. 45) basitarsi strongly compressed and very broad in lateral view; their dorsum, in profile, makes an obtuse angle before the articulation with the second tarsomere.

Sculpture. Head dorsum reticulate, with superimposed, superficial, small, sparse foveae, and with irregular, thin rugosities on its posterior fourth. Frontal carinae much more superficially reticulate near the frons. Ventral face of the head and cheeks with the same sculpture as on the posterior fourth of the head dorsum but with more longitudinal rugosities. Marginal part of the antennal scrobes with transversal rugosities. Mesosoma and pedicel reticulate and with irregular foveae separated by thin, longitudinal rugosities, less marked on the pedicel. Gaster and legs reticulate, the reticulation less impressed and the integument more shining on the centre of the first gastral sternite and on the basitarsi.

Pilosity. Body with three types of hairs: (1) appressed and thin originating from each fovea; (2) hair similar to the type (1) but thinner on the legs and on the gaster; (3) erect to suberect, thick, of variable length and surrounding the frontal carinae, sparser on the ventral face of the head, on the vertexal and pronotal spines, on the legs and on the apex of the gaster, rare on the mesosoma and pedicel; (4) long, erect, truncate on the apex of the gaster and on the coxae.

Colour. Black; frontal carinae, tarsomeres and anterolateral lamellae of the first gastral tergite reddish-brown.

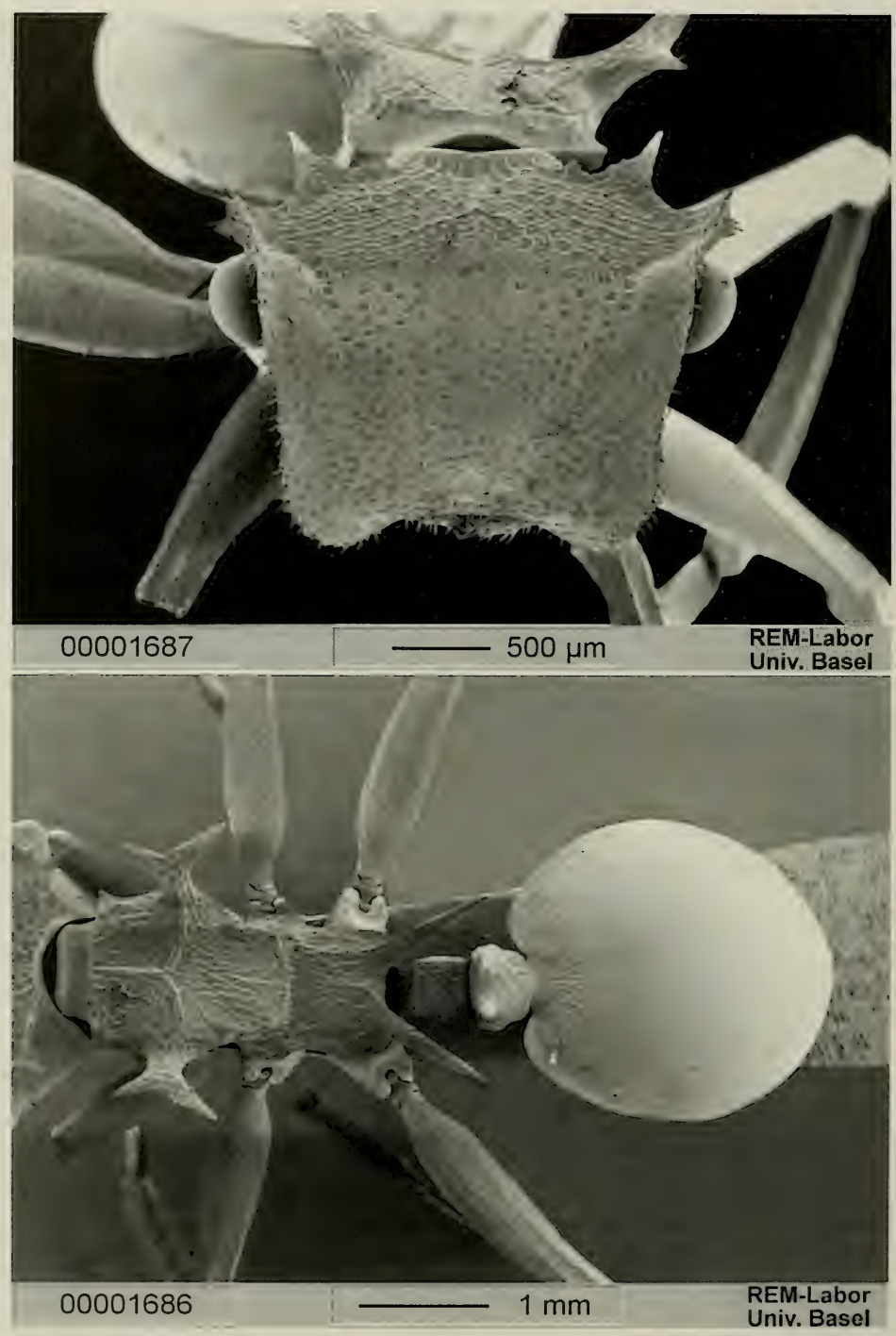


Fig. 44. *Cephalotes serraticeps* (SMITH). Worker from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 45. *Cephalotes serraticeps* (SMITH). Worker from Manaus, Brazil, hind basitarsus and tarsus in anterior view.

Measurements (in mm) and indices: TL 7.56–8.92; HL 1.60–1.84; HW 2.04–2.28; EL 0.45–0.54; PW 1.84–2.16; PeW 0.44–0.50; PpW 0.60–0.61; HBaL 1.28–1.52; HBaW 0.34–0.41; CI 123.9.127.5; PI 105.5–110.9; PPeI 418.2–432.0; PPpI 306.7–354.1; HBaI 26.6–27.0.

S o l d i e r (Fig. 46). - Differing from the worker for the following characters: head dorsum broader anteriorly than posteriorly; frontal carinae covering the cheeks, partially hiding the eyes and narrowing backwards. Vertexal angles with a broad, subtriangular tooth. Vertex with a pair of short, stout teeth. Vertexal margin deeply concave and with a short "neck". Eyes less globose.

Mesosoma. Pronotal sides with thicker and shorter spines not bifurcate at the apex. Pronotal dorsum with a pair of broad, triangular teeth.

Anterolateral lamellae of the gaster narrower.

Sculpture. Head superficially and minutely reticulate, with dense foveae on the posterior third, the foveae diminishing in size and sparser anteriorly, smaller and shallower on the frontal carinae. Ventral face of the head, mesosoma and pleurae with the same type of sculpture as on the posterior third of the head, the foveae absent on the middle of the mesopleurae and on the lower metapleurae. Peduncular segments with superficial, irregular foveae. Gaster and legs reticulate, the reticulation less impressed on the centre of the first gastral sternite and on the basitarsi. The anterior third of the first gastral tergite, in addition, is covered by superficial foveae with superimposed, superficial, longitudinal rugosities. Mid and hind femora with thin, transversal rugosities; this sculpture equally present but less impressed and oblique on the fore femora.

Pilosity. Body with four types of hairs: (1) short, appressed, thin originating from each fovea; (2) appressed and pointed on the gaster and on the legs; (3) erect to suberect, thick, slightly clavate and variable in length surrounding the head, on the mesosoma, on the peduncular segments, on the gaster and on the legs; (4) long and pointed on the two last gastral tergites and on all sternites.

Colour. Black.

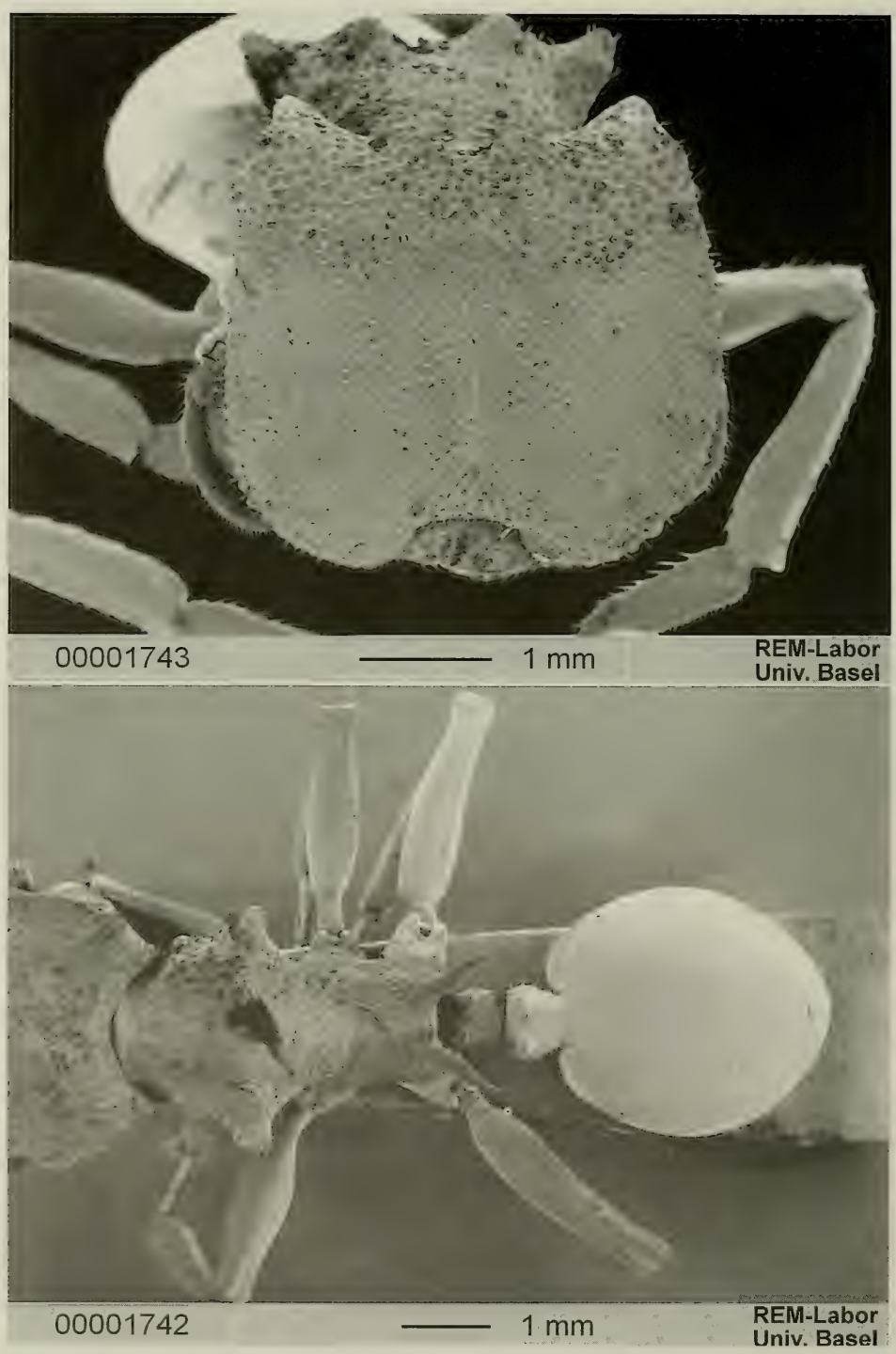


Fig. 46. *Cephalotes serraticeps* (SMITH). Soldier from Avispas, Peru: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 47. *Cephalotes serraticeps* (SMITH). Male from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 11.88; HL 2.80; HW 3.32; EL 0.68; PW 2.76; PeW 0.80; PpW 0.84; HBaL 1.84; HBaW 0.52; CI 118.6; PI 120.3; PPeI 345.0; PPpI 328.6; HBaI 28.3.

G y n e . – Head longer than broad and without disc. Vertex with a pair of subround teeth. Vertexal angles with a small subtriangular tooth. Frontal carinae with parallel sides, distinctly crenulate over their whole length; the denticles constituting the crenulation well marked and spaced. Pair ocelli obsolete and confused with the microsculpture. Eyes moderately protruding laterally.

Mesosoma, in profile, raised and flat at the height of the mesonotum. In dorsal view the sides subparallel up to the propodeum – which is much narrower – moderately bulging at the level of the alar sclerites. Pronotum abruptly sloping cranially. Scapular angles distinct, their distance shorter than the one between the pronotal spines; the latter short, pointed and obliquely directed forwards. Scutellum nearly flat, abruptly sloping caudally. Propodeum with the basal face gently sloping caudally, moderately convex and much shorter than the descending one. Descending face concave. Propodeal spines horizontal and parallel, about half as long as their distance at the apex.

Petiole sessile, with abrupt anterior face making an angle of almost 90° with the superior one. Postpetiole only slightly broader than the petiole, with short but distinct anterior face separate by a weak, marginate angle from the superior one; ventral postpetiolar tooth moderately prominent but marked. Petiole and postpetiole without lateral spines or expansions.

Gaster nearly twice longer than broad, poorly marginate anteriorly; laterally the margination does not reach the stigma of the first segment.

Fore tibiae moderately, mid and hind tibiae strongly compressed laterally. Hind basitarsi 1 strongly compressed and very broad (more than in the *alfaroi* workers) in lateral view; its dorsal side, in profile, makes an obtuse angle before the articulation with the second tarsomere.

Fore wings. Distal part of *R+Sc* depigmented; *2r* well visible; *Rsf5* connected with *R1* partially outlining the distal border; *A*, *Cu-A*, *Cu-A1* and *Mf4* well marked and reaching the distal border; *cu-a* interrupted in the middle.

Hind wings: *R*, *M+CuA*, *1A*, *CuA*, *r-m1* and *M* well marked; distal parts of *CuA* and *M* vestigial and nearly reaching the distal border. Two or three additional *r-m* present.

Sculpture. Body largely smooth and shining, the sculpture relatively uniform, composed essentially of deep round, foveae. The foveae much denser on the head capsule and on the pedicel (their distance equal to their maximum diameter) than on the mesosoma (distance between the pits ca. twice their maximum diameter) and on the gaster where they are much less impressed, concentrated on the anterolateral portion of the first tergite and sparser (distance between the pits often three times their diameter). Posterior border of the first gastral tergite, first gastral sternite and remaining gastral segments finely reticulate-punctate with superimposed shallow foveae. Mandibles longitudinally striate. Legs and antennal scapes minutely reticulate-punctate.

Pilosity. Besides the minute foveal hairs, the pilosity consists of long, clavate hairs around the antennal scrobes (more clearly clavate than in *alfaroi*). Similar clavate hairs on the sides of the mesosoma and on the scutellum. A few truncate or pointed hairs on the propodeum. Pedicel and dorsal face of the gaster with truncate, subtruncate, or pointed sparse hairs. Sparse, acuminate hairs on the first gastral tergite. Distal half of the first dorsally and remaining gastral sternites wholly with long, pointed hairs. Mandibles and antennae covered by thick, appressed, truncate or subtruncate hairs. Legs similarly covered by suberect to subdecumbent clavate or truncate hairs.

Colour. Black very shining over most of the body, opaque only on the lateral and posterior border of the first and on the following segments of the gaster and on the appendages where the microscopic reticulation-punctuation is present. Wings yellowish transparent with opaque brown distal part of the submarginal and of the marginal cells. Hairs golden.

Measurements (in mm) and indices: TL 15.50–16.00; HL 2.88–3.00; HW 3.00–3.10; EL 0.68; PW 2.80; PeW 0.92–0.96; PpW 1.04–1.08; HBaL 1.80–1.84; HBaW 0.60–0.64; CI 103.3–104.2; PI 107.1–110.7; PPeI 291.7–304.3; PPpI 259.2–269.2; HBaI 33.3–34.8.

M a l e ? (Fig. 47) (previously undescribed, description based on a specimen collected in the same biotope where *serraticeps* workers have been collected). - Head (eyes included) more than 1/3 broader than long. Vertexal angles, internally , with a short, triangular denticle and with a broad, triangular tooth close to the posterior border of the eye. Vertexal margin prolonging backwards into a broad "neck". Vertex dorsally convex and bearing salient ocelli. Compound eyes convex, in the middle of the sides of the head. Frontal carinae low, not reaching the impair ocellus. Frons flat posteriorly, slightly declivous anteriorly. Clypeus-convex posteriorly, marked by a transverse, median angle sloping anteriorly. Mandibles slender, laterally with a superficial carina. Scapes thick and short, not reaching the posterior border of the eyes.

Mesosoma. Pronotum in dorsal view anteriorly protruding, and with the sides diverging backwards. Pronotal dorsum separate from the sides by a transverse carina. Mesonotum convex in side view; Mayrian furrows impressed. Scutellum as high as the mesonotum, its sides converging posteriorly. Basal face of the propodeum much lower than the scutellum; dorsum of the basal face sloping backwards, but differentiate from the declivous one; sides of the basal face gently converging backwards, without denticles or teeth. Declivous face with converging sides, laterally and medially marked by a pair of longitudinal carinae.

Petiole with truncate anterior face; petiolar sides unarmed and gently converging posteriorly. Postpetiole broader than the petiole; postpetiolar sides bearing a round denticle in their anterior third.

Gaster with its maximum width at the posterior border of the first segment, almost three times broader than its articulation with the postpetiole.

Genitalia and subgenital plate as in Fig. 48.

Sculpture. Head dorsum reticulate; posterior half and sides of the head with irregular, slightly longitudinally oriented reticulate rugosities; this sculpture more superficial and the inter-reticular depressions smaller on the frons. Ventral part of the head with the same type of sculpture as on the vertexal angles and, around the eyes, with short, transversal rugosities. Pronotal dorsum, mesonotum, scutellum and basal face of the propodeum reticulate and with dense, irregular foveae with marked border. Sides of the pronotum, posteriorly, reticulate and with irregular, longitudinal rugosities. Pleurae reticulate and with longitudinal rugosities more regular on the metapleurae; lower mesopleurae with additional, irregular foveae. Declivous face of the propodeum, anterior third of the petiole and of the postpetiole reticulate and with irregular rugosities; the rugosities longitudinal on the sides of the petiole and postpetiole. First gastral tergite superficially reticulate; the same sculpture but more superficial and slightly shining on the remaining tergites, on the sternites and on the legs.

Pilosity. Body with two types of hairs: (1) flexuous, long, pointed hairs, more dense on the head and on the mesosoma, sparser on the pedicel and on the gaster; (2) shorter than the type (1) hairs, decumbent and dense on the legs, sparse on the scapes; (3) short, thin, on the antennae.

Colour. Black.

Measurements (in mm) and indices: TL 10.10; HL 1.36; HW 1.68; EL 0.65; PW 1.44; PeW 0.65; PpW 0.79; CI 123.5; PI 116.7; PPeI 228.6; PPpI 182.3.

M a t e r i a l e x a m i n e d : holotype gyne without locality label (presumably Tefé, Amazonas, Brazil) (BMNH). **B r a z i l** : A m a p á : Curiaú, 19.XI.1981, 1 worker, Gorayeb [MPEG]; Highway BR. 156, km 14, border of Rio Matapi, 31.XI.1981, 1 worker [MPEG]; Serra do Navio, IX.1957, 1 worker, J. Lane [MZSP]. A m a z o n a s : 1 worker, H. W. Bates (ZSMC); Humaitá, I.1975, 1 gyne, A. Scivittaro [MZSP]; Reserva Flor. A. Ducke, 2° 55' S, 59° 59' W, 19.I, 26.VIII, 12.XI.1982, 3 workers, 1 small soldier, Adis et al. [INPA, CPCC]; same locality and collectors, 21.VIII.1991, 2 workers [INPA]; same locality and collectors, 23.II.1992, 26.VIII.1992, 4 workers [INPA]; same locality, 22–26.I.1996, 1 male, M. L. de Andrade [INPA]; Tarumã-Mirim, 08.III.1976, 1 worker, J. Adis [INPA]. P a r á : Belém, APEG, 09.IV.1969, 1 worker, N. Rosa [MZSP]; Serra Norte, border of the Salobo, 24.II.1984, 1 gyne, A. G. R. G. Ferreira [MPEG]; Tucuruí, left side, 14. III. 1979, 1 worker, 1 soldier, W. L. Overal [MPEG]. M a r a n h ã o : Alto Turiaçu, Aldeia Gurupiuna, 16–19.II.1990, 3 workers, H. Queiroz [MPEG]; R o n d ô n i a : Vilhena, 02.VIII.1983, 1 worker, A. Y. Harada [INPA].

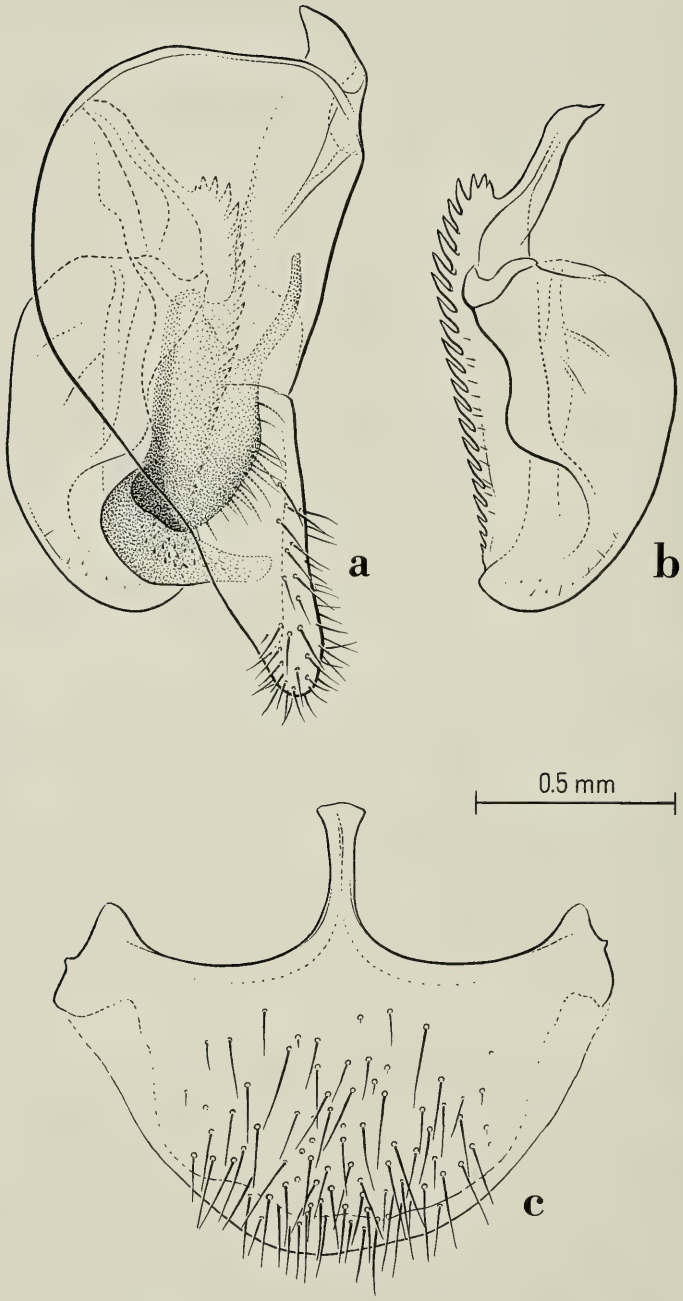


Fig. 48. *Cephalotes serraticeps* (SMITH). Male from Manaus, Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Peru: Madre de Dios: Avispas, 400 m, 10–30.IX.1962, 1 soldier, PEÑA [MCZC].

Discussion. - We find *serraticeps* differing from all syntypes and from other *alfaroi* specimens we have seen for the characters already listed in the diagnosis. Since these characters are invariant in all workers and gynes of the *atratus* clade and in most *Cephalotes* species we have seen, it is inevitable to consider *serraticeps* as a valid species separate from *alfaroi*.

FERNÁNDEZ et al. (1996) report this species from Colombia with doubt.

Distribution: Brazil, Peru (and Colombia?).

Cephalotes oculatus (SPINOLA)

Figs. 49, 50, 51, 52, 387 (top)

Cryptocerus oculatus SPINOLA, 1853: 48. Worker. Original description. Type locality: Belém (Pará, Brazil). Type material: presumably lost, not in the SPINOLA collection (CASOLARI & CASOLARI MORENO, 1980).

Cryptocerus æthiops SMITH, 1854: 216, pl. 20 fig. 9. Worker. Original description. Type locality: Brazil. Type material: a worker (holotype), without locality label in the BMNH, examined. Synonymy by SMITH, 1858: 188.

Cephalotes oculatus (SPINOLA), EMERY, 1914: 39. First combination in *Cephalotes*.

Eucryptocerus oculatus (SPINOLA), KEMPF, 1951: 130, figs. 108, 112–114. Worker. First combination in *Eucryptocerus*.

Diagnosis. - A member of the *atratus* clade characterised by the wide interocular distance and by the propodeum and mesonotum clearly marginate (as opposed to weakly or indistinctly marginate in the closest species).

Worker (Figs. 49, 387 top) (description of KEMPF, 1951). - "Length 7.7–8.9 mm. Distance between the most anterior projection of the frontal carinae and the apex of the internal occipital spine somewhat shorter than the interocular width. The pair of teeth on the vertex well developed. The internal occipital spines sometimes obliquely truncate or bidenticulate at apex. Upper surface of head foveolate only on posterior half, the foveolae, rather deeply impressed behind the vertical teeth. Lower surface of head with large and deeply impressed areoles. Thorax more sparsely and superficially foveolate. Scapular spines strong. Medial pronotal spines well developed. Mesonotum submarginate laterad. Basal face of epinotum rather flat, its sides marginate in front. Epinotal spines strong, usually as long as the basal face, somewhat divergent and raised upward. Basitarsus of middle and hind legs, prismatic almost as deep as broad. Petiole broader than long: its sides converging caudad. Gaster emarginate in front, the first tergite subfulgid discad, anterolaterally with projecting, large angulate lobes. Erect setae confined to femora, mandibles, lower surface of head and gaster."

Measurements (in mm) and indices: TL 7.76–8.68; HL 1.88–2.04; HW 2.41–2.64; EL 0.43–0.48; PW 2.41–2.72; PeW 0.61–0.68; PpW 0.66–0.80; HBaL 0.92–1.04; HBaW 0.19–0.20; CI 128.2–135.5; PI 97.0–100.0; PPeI 400.0–406.5; PPpI 334.7–364.7; HBaI 19.2–20.6.

Gyne (previously undescribed). - Head subquadrate, without disc. Frons convex. Frontal carinae converging anteriorly and straight up to the vertexal angles. Frontal carinae superficially crenulate and with a small tooth in the middle. Vertexal angles with two pairs of teeth, the anterior pair behind the eyes and smaller than the posterior one. Vertex marked by a pair of large, triangular teeth. Mandibles only superficially angulate.

Mesosoma. Humeral angles bearing a thick, pointed tooth. Pronotal crest well marked and interrupted in the middle by a superficial impression, slightly higher around the median interruption and superficially crenulate. Mesonotum and scutellum nearly flat in side view. Lower mesopleurae with a stout, small tooth. Basal face of the propodeum much lower than

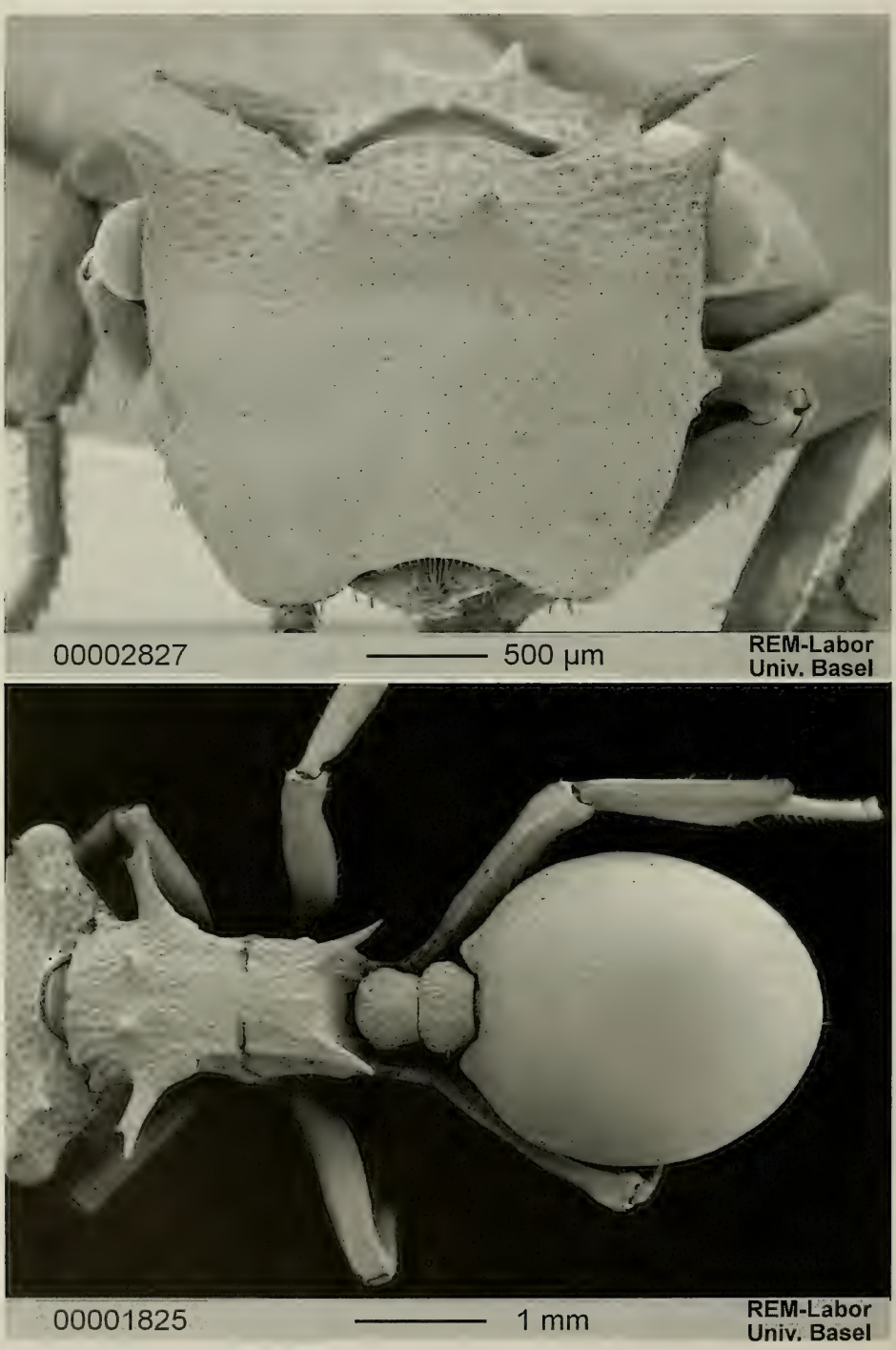


Fig. 49. *Cephalotes oculatus* (SPINOLA). Worker from Pará, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

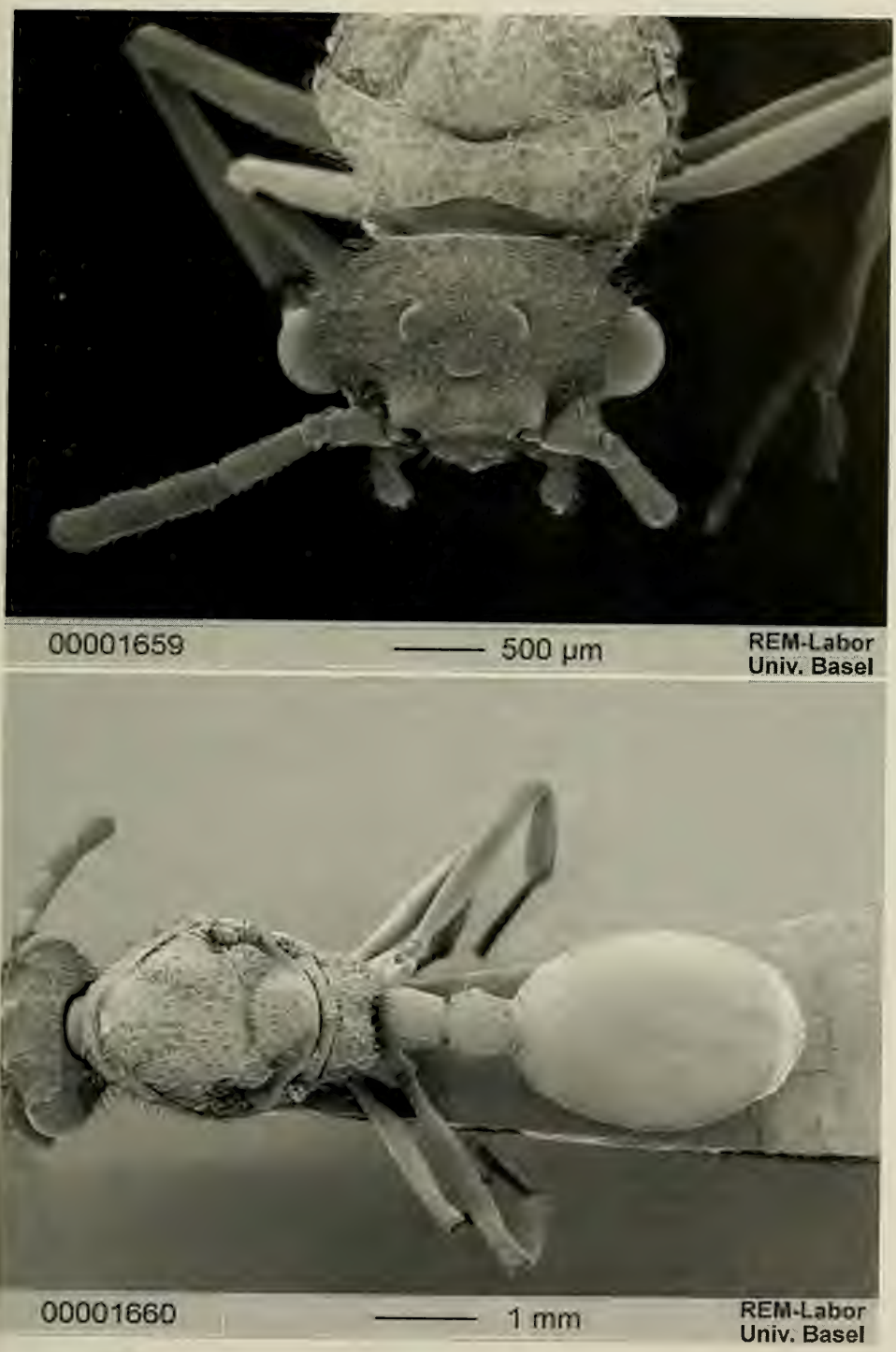


Fig. 50. *Cephalotes oculatus* (SPINOLA). Male from Belém (Pará), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

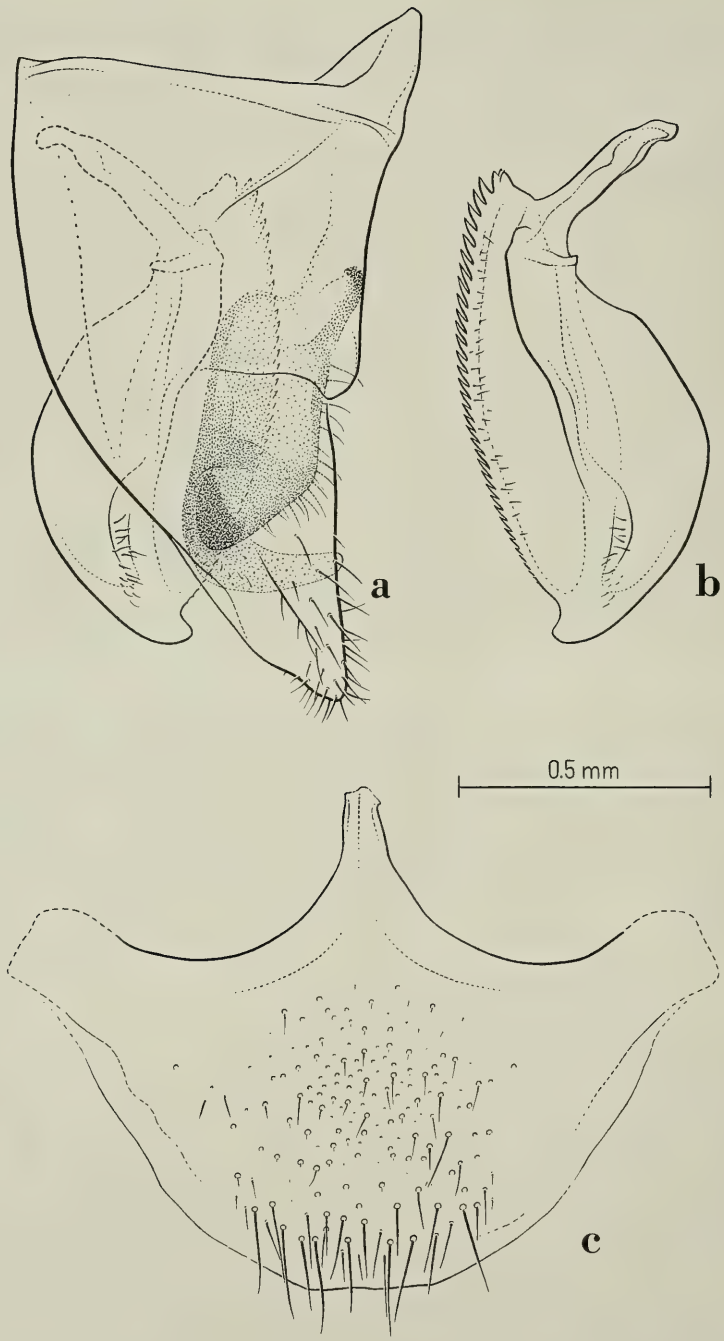


Fig. 51. *Cephalotes oculatus* (SPINOLA). Male from Belém (Pará), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

the scutellum and short; its sides with a pair of short, thick, slightly diverging spines directed backwards. Sides of the declivous face of the propodeum converging posteriorly.

Petiole with differentiate anterior and posterior faces; anterior face truncate, posterior face sloping posteriorly. Petiole unarmed and with posteriorly converging sides. Postpetiole convex dorsally and laterally; its maximum width in the anterior half.

Gaster with a thin lateral margin not reaching the first gastral stigma.

Legs. Fore coxae round. Mid and hind femora not marked by an angle. Mid and hind basitarsi compressed laterally; their diameter constant through the whole length.

Sculpture. Head minutely reticulate and with superficial and variably clumped foveae, larger on the vertex. Ventral part of the head and propleurae with the same type of sculpture as on the vertex but with larger and deeper foveae. Pronotal dorsum, mesonotum, basal face of the propodeum and upper mesopleurae minutely reticulate and with foveae as broad as on the vertex, more superficial on the mesonotum. First gastral tergite with sparse, oval, superficial foveae and impressed by two sets of very thin, superficial, concentric rugulosities originating respectively at about one third and two thirds of the length of the sclerite. Lower mesopleurae, metapleurae, declivous face of the propodeum, first gastral sternite and legs reticulate; remaining tergites and sternites reticulate and irregularly rugulose. Lower mesopleurae with rare, superficial foveae. Anterior and posterior faces of the tibiae with faint, thin, longitudinal rugosities.

Pilosity. Each fovea bearing a thin, appressed hair; border of the frontal carinae and remaining body surfaces with additional, sparse, long, slightly clavate, erect and suberect hairs, longer and denser on the legs and on the apex of the gaster.

Colour. Black. Antennae and tarsomeres brown. First gastral tergite superficially shining.

Measurements (in mm) and indices: TL 13.94; HL 2.56; HW 3.00; EL 0.60; PW 3.12; PeW 1.00; PpW 1.16; HBaL 1.32; HBaW 0.27; CI 117.2; PI 96.1; PPeI 312.0; PPpI 269.0; HBaI 20.4.

M a l e (Fig. 50) (previously undescribed). - Head (eyes included) about 1/3 broader than long. Vertexal angles medially with a curved carina continuing frontally up to the internal border of the eyes. Vertexal margin prolonged backwards into a neck. Vertex and compound eyes as in *opacus*. Frontal carinae high, broad, with irregular border and posteriorly obtuse and continuing backwards as a thin, irregular frontal margin, not reaching the impair ocellus. The rest as in *opacus*.

Mesosoma. Pronotum and mesonotum similar to *opacus* but much broader. Basal face of the propodeum gently convex, medially impressed, and sloping backwards less abruptly than in *opacus*; sides of the basal face gently converging backwards, with a carinate, almost round tooth on the posterior half. Declivous face marked, laterally, by a pair of longitudinal, convergent carinae.

Petiole and postpetiole cylindrical, shorter and more convex dorsally than in *opacus*; anterior border of the petiolar face truncate, weakly concave in the middle and not carinate dorsally. Postpetiole laterally tuberculate.

Gaster with its maximum width at the posterior border of the first segment, three times broader than its articulation with the postpetiole.

Genitalia and subgenital plate as in Fig. 51.

Wings as in Fig. 52.

Sculpture. As in *opacus* but with the following differences: foveae more regular and deeper on the head, pronotum, mesonotum and scutellum; basal face of the propodeum with deeper, denser, irregular foveae; declivous face of the propodeum with thick, sparse, longitudinal rugosities; centre of the mesopleurae with superficial foveae; pedicel with sparse superficial depressions superimposed by irregular, longitudinal rugosities; legs less shining than in *opacus*.

Pilosity. As in *opacus*.

Colour. Head, mesosoma and pedicel opaque black. First gastral tergite and coxae brown, remaining tergites and sternites lighter. Legs dark ferrugineous with darker femora.

Measurements (in mm) and indices: TL 8.60–8.84; HL 1.28–1.32; HW 1.56–1.64; EL 0.56–0.59; PW 1.48–1.56; PeW 0.60–0.66; PpW 0.68–0.72; HBaL 1.24; HBaW 0.16; CI 121.9–124.2; PI 105.1–105.4; PPeI 236.4–246.7; PPpI 216.7–217.6; HBaI 12.9.

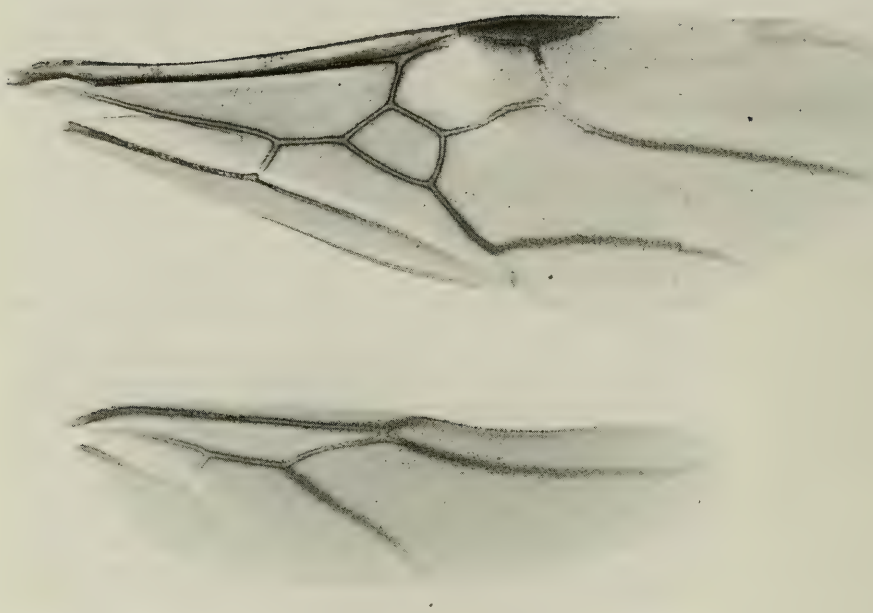


Fig. 52. *Cephalotes oculatus* (SPINOLA). Male from Belém (Pará), Brazil, fore and hind wings.

Material examined. - **Brazil**: no further locality, 1 worker (holotype of *aethiops*) [BMNH]; no further locality, 1 worker [ZSMC]. Rio Negro, 1 worker [ZSMC]. Amapá: Serra do Navio, 23.IX, 03.X.1957, 17 workers, [MCZC, MZSP]; same locality, XI.1959, XI.1960, 33 workers, P. BICELLI [MZSP]. Pará: no further locality, 6 workers, GOELDI [MZSP, NHMB, MHNG]; idem, 1 worker, ARNOLD [MCZC]; Belém, 1954, 3 workers, SEFER [MZSP]; same locality, 12–19.VIII.1962, 15 worker, K. LENKO [MZSP]; same locality, 07.XI.1974, 3 workers, D. DIAS [MZSP]; same locality, Inst. Agron. Norte, 06–19.IV.1963, 3 workers, F. G. WERNER [MCZC, MZSP]; same locality, APEG, 17.VII.1969, 1 gyne, N. ROSA [MZSP]; Belém, Fazenda Velha, 10.I.1979, 1 worker, A. F. RAMOS [MPEG]; Óbidos, 20.XI.1907, 1 gyne, DUCKE [MPEG]; Acará, different dates and collectors, 6 workers [MPEG]; Bujaru, 3.III. & 21.IV.1979, 23 workers, A. F. RAMOS & R. B. NETO [MPEG]; Rio Gelado, 19.IX.1985, 5 workers, M. ZANUTO [MPEG]; N1 Floresta (Serra Norte), 31.X–6.XI.1985, 3 workers, F. F. RAMOS [MPEG]; Fofoca (Serra Norte), different dates and collectors, 13 workers [MPEG]; Manganês (Serra Norte), 27.VI.1985, 5 workers, M. ZANUTO [MPEG]; Pojuca (Serra Norte), different dates and collectors, 9 workers [MPEG]; 3 Alfa (Serra Norte), different dates and collectors, 9 workers [MPEG]; Caldeirão (Serra Norte), different dates and collectors, 17 workers [MPEG]; Tucuruí, different dates and collectors, 19 workers [MPEG]; Itaituba, Parque Nacional da Amazônia, 14–16.XI.1978, 1 worker, 1 gyne, R. B. NETO & W. L. OVERAL [MPEG]; Benevides, 21.VI.1980 & 26.VII.1992, 2 workers, M. F. TORRES & C. N. ARCANJO [MPEG]; Ourém, 29.X.1990, 2 workers, P. TADEU [MPEG]; Monte Dourado, 2.XI.1979, 6 workers, R. B. NETO [MPEG]; Mocambo, different dates and collectors, 38 workers [MPEG]; Utinga, highway near Belém, 3 workers, 06.VIII.1962, P. F. DARLINGTON [MCZC, MZSP]; Utinga, several dates and collectors,

37 worker [MPEG, MZSP]; Ben Fica, 13.VIII.1962, 1 worker, W. L. BROWN [MCZC]; Reserva Guamá, 28.V, 03.XI.1966, 8 workers, 2 males [MZSP]; Carajás, 01.VIII.1983, 3 workers, W. BENSON [MZSP]; Norte de Carajás, VII-VIII.1985, 14 workers, C. R. F. BRANDÃO & W. BENSON [MZSP]; Aldeia Coraci, 11 km W Canindé, Rio Gurupi, XII.1964, 1 worker, B. MALKIN [MZSP], Canindé, Rio Gurupi, 07–15.IV.1963, 4 workers, B. MALKIN [MZSP]; Cachoeira do Espelho, Rio Xingu, 21–28.X.1986, 6 workers, F. C. VAL [MZSP]; Caldeirão, Rio Itacaiunas, 23 & 25.VIII.1983, 20 workers, W. BENSON [MZSP]; Aldeia Araçu, Igar. Urupi-Una, 31.I, 29.V.1963, 6 workers, B. MALKIN [MZSP]; Icoaraci, 03.VIII.1962, 2 workers, P. F. DARLINGTON [MZSP]; Ananindeua, I.1963, 6 workers, MACHADO & PEREIRA [MZSP]. Bahia: Medicilândia, 30.VII–13.VIII.1992, 4 workers, A. J. S. ARGOLO [CPCC, USNM].

Discussion. - This distinctive species, unequivocally different from all congeners for the wide interocular distance, appears to be confined to the northern part of Brazil. A worker from Pará in NHMB and three out of four from Medicilândia (Bahia) have propodeal spines long about half the normal size for this species. Two workers from Tucuruí (Pará) in MPEG are completely destitute of propodeal spines. Other workers from the same locality, however, have normally developed propodeal spines.

Distribution: Brazil.

Cephalotes opacus SANTSCHI

Figs. 53, 54, 55, 56, 57, 58

Cephalotes opacus SANTSCHI, 1920: 147. Worker. Original description. Type locality: St. Jean du Maroni (French Guyana). Type material: holotype worker (unique), without head in NHMB (examined).

Eucryptocerus opacus (SANTSCHI), KEMPF, 1951: 131, fig. 107. Worker. First combination in *Eucryptocerus*.

Eucryptocerus placidus (F. SMITH), KEMPF, 1959: 92. Partim. Nec SMITH, 1860. Misidentification.

Cephalotes abdominalis SANTSCHI, 1929: 302. Worker. Original description. Type locality: St. Jean du Maroni (French Guyana). Type material: lost; the original pin is still in the NHMB but no ant is glued to the label nor can it be found in the drawer. New synonym.

Eucryptocerus abdominalis (SANTSCHI), KEMPF, 1951: 129, fig. 115. Worker. First combination in *Eucryptocerus*.

Eucryptocerus opacus, KUGLER, 1978: 473, figs. 192–194. Worker, sting.

Eucryptocerus abdominalis (SANTSCHI), LATTKE, 1985: 83.

Eucryptocerus. BOLTON, 1994: figs. 214, 215. Worker.

Diagnosis. - A member of the *atratus* clade appearing as sister species of *placidus*. Its main apomorphy, in the worker, are the short, cylindrical propodeal spines.

Worker (Fig. 53). - Head subquadrate. Border of the frontal carinae irregularly crenulate, with a small, median denticle. Eyes globose, behind of the scrobes. Vertexal angles with two pairs of teeth with lamellaceous border; the anterior tooth smaller and separate from the posterior one by a deep notch. Vertexal margin prolonged backwards into a visible neck. Vertex with a pair of denticles, more developed in larger specimens. Mandibles, laterally, with a superficially carinate tumulus.

Mesosoma. Anterior pronotal border with a superficial incision in the middle and with a developed scapular angle laterally. Anterior third of the pronotal sides straight, second third with a pair of long spines with bidenticulate tip, posterior third gently converging behind. Pronotal dorsum with a pair of denticles more developed in large specimens. Pronotal suture

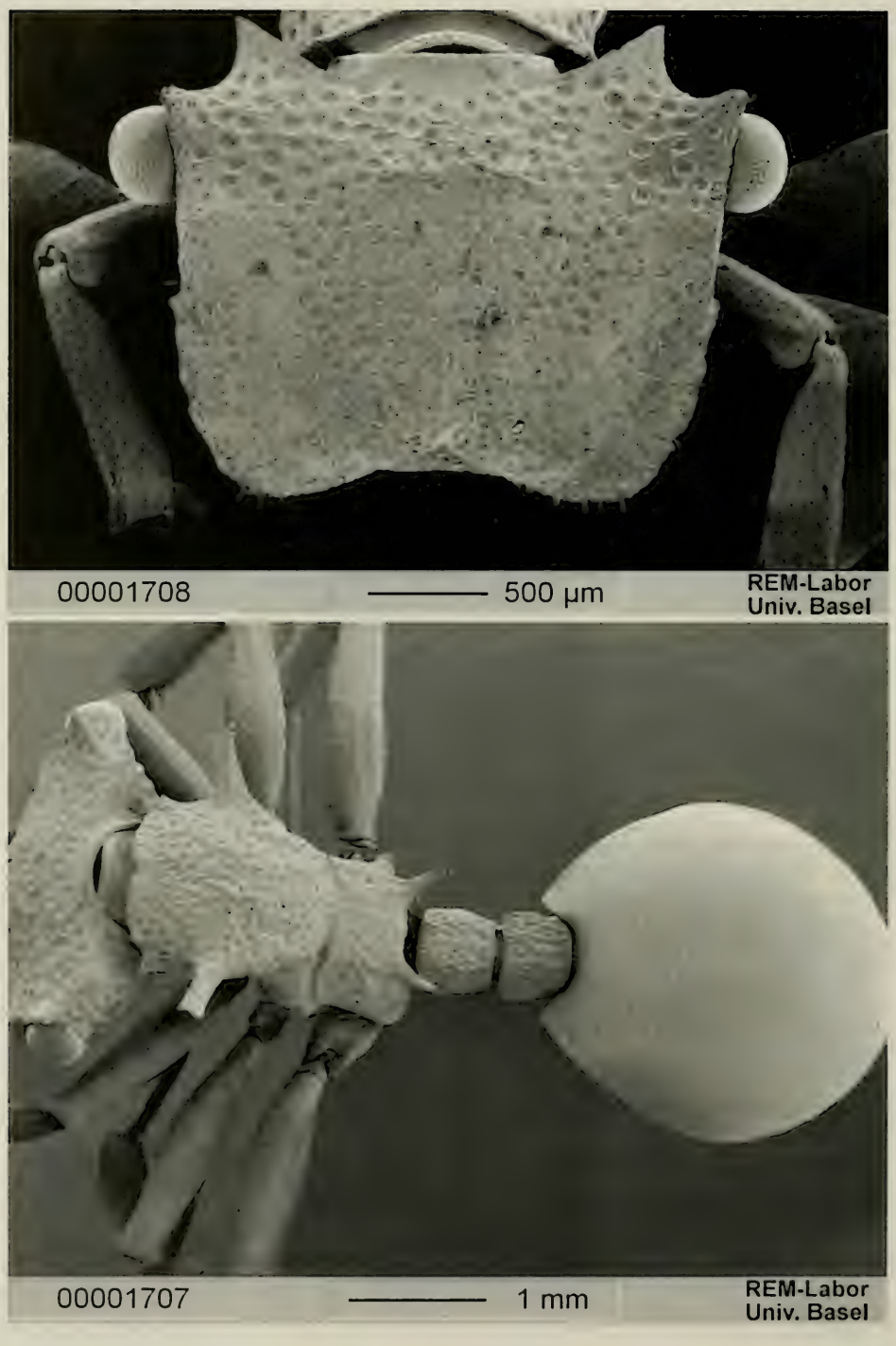


Fig. 53. *Cephalotes opacus* SANTSCHI. Worker from Linhares (Espírito Santo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

marked on the sides. Mesonotal sides unarmed, superficially marginate and gently converging posteriorly. Propodeal suture well impressed, less marked in the middle. Basal face of the propodeum with straight, weakly marginate sides and separate from the declivous one by a pair of cylindrical spines. Propodeal spines as long as half or less than half of the maximum length of the basal face of the propodeum. Declivous face of the propodeum straight and laterally separate from the broad metapleura by a carina.

Petiole subcylindrical, with truncate anterior face, dorsally and laterally unarmed and gently converging posteriorly. Postpetiole slightly higher than the petiole; anterior half of the postpetiolar sides convex or truncate, posterior half converging backwards.

Gaster with a pair of anterior lamellae or simply shortly marginate.

Legs. Mid and hind femora without angle or denticle medially but with a pair of faint longitudinal carinae on the two posterior thirds. Hind basitarsi long, laterally compressed and slightly broadening at the base.

Sculpture. Head entirely minutely and superficially reticulate and with foveae diminishing in size anteriorly, denser on the on their posterior third, very superficial on the frons and on the hypostomal area of some specimens. Mesonotum minutely reticulate and with variably distributed and impressed foveae; in some specimens the foveae are smaller, sparser and more superficial on the mesonotum and on the propodeum. Pedicel minutely reticulate and with dense, mall foveae. Gaster and legs reticulate. Femora with thin, short, irregular, superficial rugosities. Centre of the first gastral tergite and sternite superficially reticulate and shining.

Pilosity. Each fovea with a thin, short, appressed, pointed hair; similar hairs but not originating from the foveae on the legs and on the gaster. Anterior border of the frontal carinae, vertexal angles, pronotal spines and legs with rare, short, suberect, clavate hairs; similar hairs but longer and slender on the legs and on the posterior border of the gastral tergites and sternites. Sternites with long, pointed hairs.

Colour. Black and variably opaque. Frontal carinae with two pairs of infuscate dark-reddish, opaque maculae. Border of the vertexal angles, of the gastral lamellae and tarsomeres dark-ferrugineous.

Measurements (in mm) and indices: TL 6.56–8.70; HL 1.54–2.40; HW 1.94–2.40; EL 0.40–0.48; PW 1.68–2.28; PeW 0.50–0.62; PpW 0.52–0.60; HBaL 0.96–1.20; HBaW 0.19–0.25; CI 115.6–125.9; PI 104.0–115.5; PPeI 336.0–392.8; PPpI 297.1–340.3; HBaI 19.8–21.4

S o l d i e r (Fig. 54). - Differing from the worker for the following characters: frontal carinae gently converging in front of the eyes. Vertexal teeth smaller and without lamellaceous border. Vertex with a pair of larger denticles. Eyes less globose.

Mesosoma. Notch on the anterior pronotal border almost absent. Pronotal sides with thicker and shorter spines. Pronotal dorsum with a pair of broad, flat, triangular teeth. Mesonotal sides unarmed or slightly convex, superficially marginate and gently converging posteriorly. Propodeal suture deeply impressed.

Gaster with a pair of lamellae of variable size.

Measurements (in mm) and indices: TL 10.32–10.60; HL 2.40–2.48; HW 3.00; EL 0.56–0.60; PW 2.84–2.96; PeW 0.72–0.76; PpW 0.80–0.84; HBaL 1.24–1.32; HBaW 0.28; CI 121.0–125.0; PI 101.3–105.6; PPeI 373.7–411.1; PPpI 352.4–355.0; HBaI 21.2–22.6.

G y n e (Fig. 55) (previously undescribed). - Head subquadrate, slightly broader than long and with subparallel sides. Frons gently convex. Frontal carinae converging anteriorly and straight up to the vertexal angles. Frontal carinae broadly crenulate and with a small tooth in the middle. Vertexal angles with a pair of small teeth separate by a concavity from a low, anterior angle, the angle round and poorly projecting. Vertex marked by a pair of triangular teeth. Mandibles as in *oculatus*.

Mesosoma. Humeral angles bearing a thick, pointed tooth. Pronotal crest well marked, high, with crenulations and interrupted in the middle by a superficial impression. Mesonotum, scutellum, lower mesopleurae and sides of the declivous face of the propodeum as in *oculatus*. Basal face of the propodeum much lower than the scutellum and short; its sides with a pair of subtriangular spines, slightly diverging backwards.

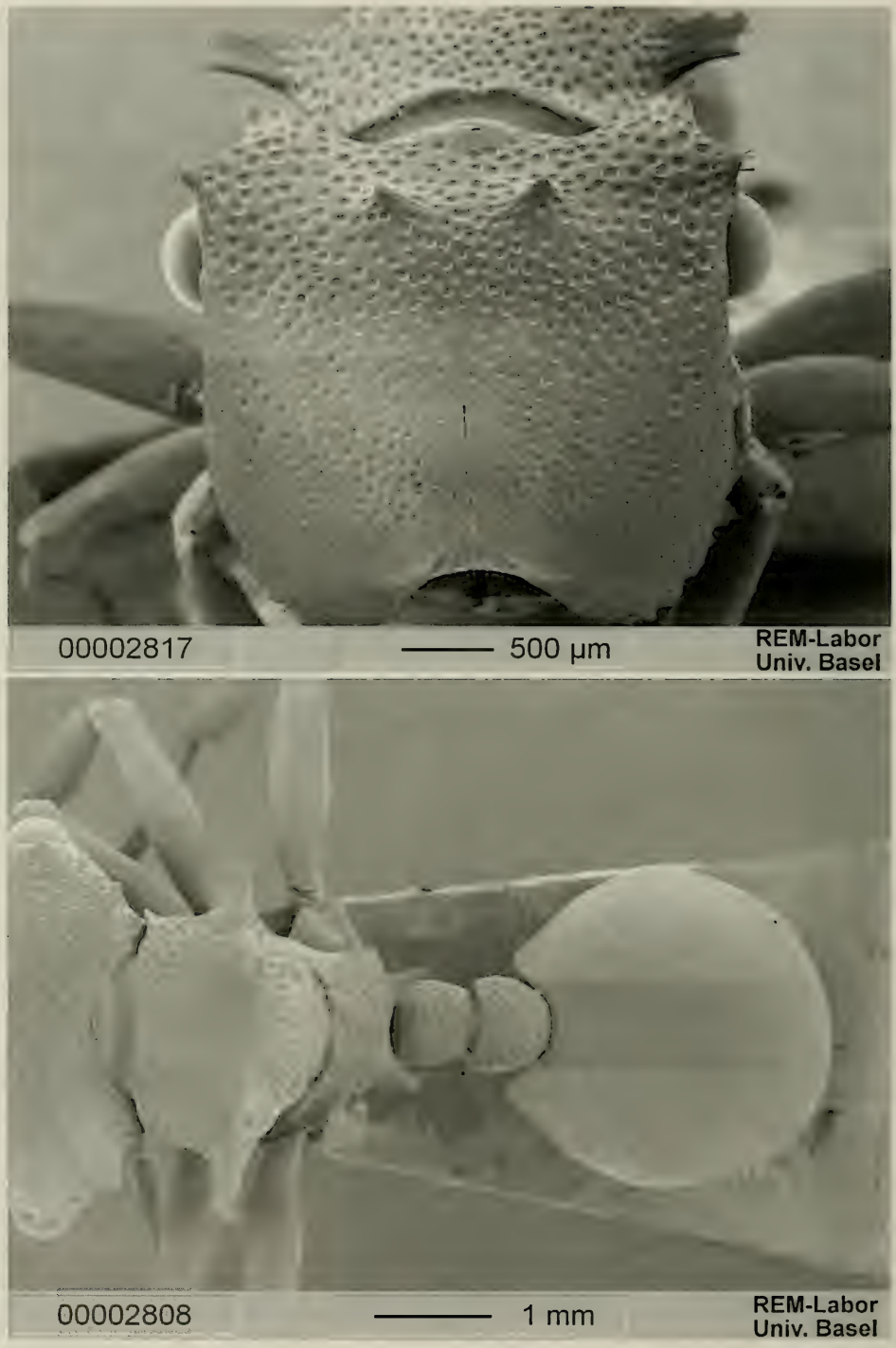


Fig. 54. *Cephalotes opacus* SANTSCHI. Soldier from Leticia (Amazonas), Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

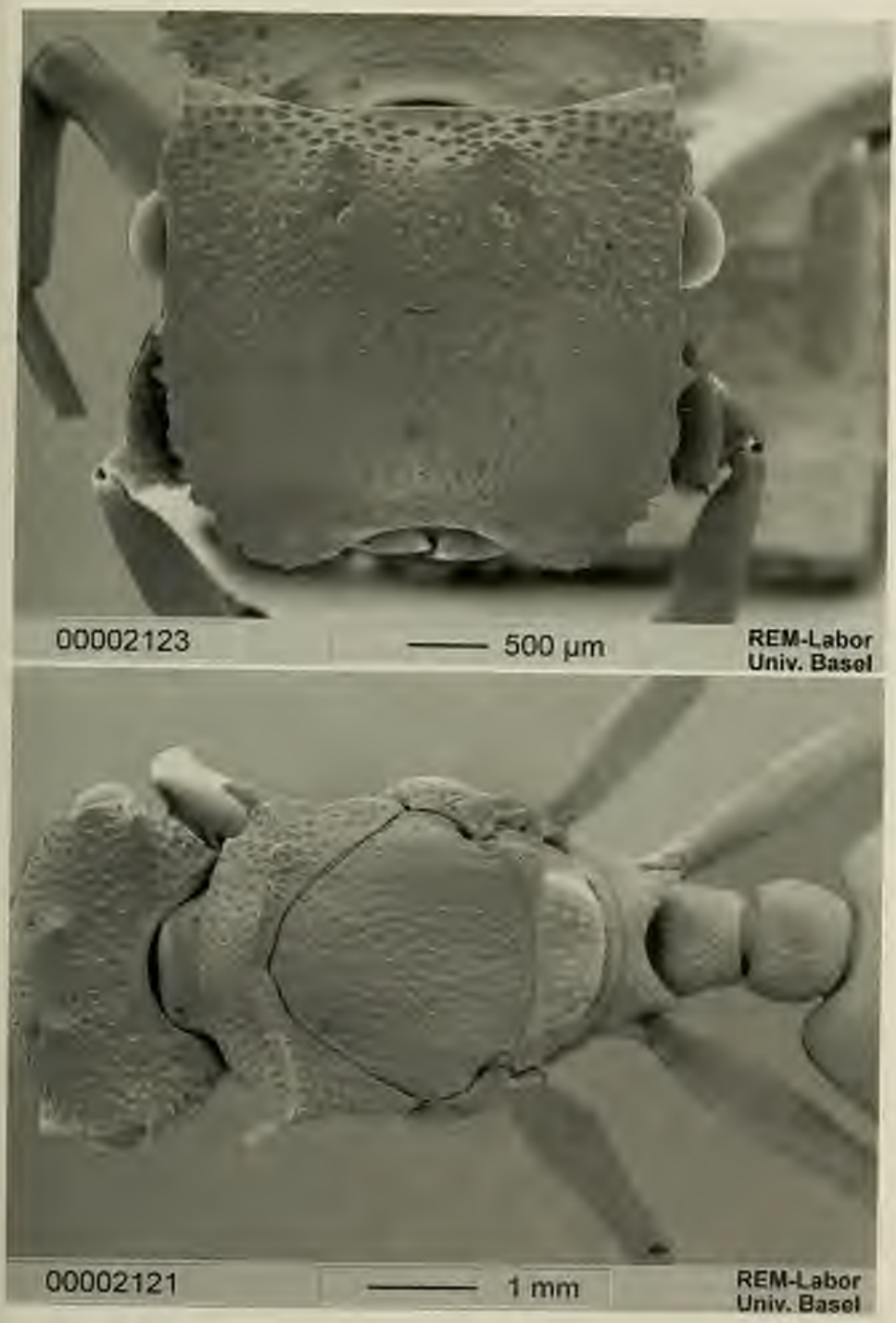


Fig. 55. *Cephalotes opacus* SANTSCHI. Gyne from Leticia (Amazonas), Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

Petiole with differentiate anterior and posterior faces; anterior face truncate, posterior face gently sloping posteriorly. Petiole unarmed and with the sides weakly converging posteriorly. Postpetiole convex dorsally; sides of the postpetiole slightly convex

Gaster with a thin lateral margin not surpassing the first gastral stigma posteriorly.

Legs as in *oculatus*.

Sculpture as in *oculatus* differing only in the size of the foveae, generally larger and sparser on the lower mesopleurae.

Pilosity as in *oculatus*.

Colour. Black. Tarsomeres brown.

Measurements (in mm) and indices: TL 14.52; HL 2.64; HW 3.04; EL 0.64; PW 3.24; PeW 0.96; PpW 1.08; HBaL 1.44; HBaW 0.31; CI 115.1; PI 93.8; PPeI 337.5; PPpI 300.0; HBaI 21.5.

M a l e ? (Fig. 56) (previously undescribed, description based on a specimen collected in the same biotope where *opacus* workers have been collected). - Head (eyes included) slightly less than 1/3 broader than long. Vertexal angles, medially, with a broad, triangular denticle continuing into a longitudinal, incomplete carina almost reaching the internal border of the eye. Vertexal margin prolonging backwards into a broad neck. Vertex dorsally gently convex and bearing salient ocelli. Compound eyes convex, in the middle of the sides of the head. Frontal carinae high, slightly convex, broad, not reaching the impair ocellus but diverging backwards into a thin, irregular margin. Frons flat posteriorly, slightly declivous anteriorly. Clypeus convex posteriorly and with almost truncate anterior face. Mandibles slim, laterally with a superficial carina. Scapes thick and short, not reaching the posterior border of the eyes. Funiculi thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards. Mesonotum convex in side view; only pair Mayrian furrows impressed and visible. Scutellum convex and higher than the mesonotum, its sides converging posteriorly. Basal face of the propodeum much lower than the scutellum; dorsum of the basal face sloping backwards, but differentiate from the declivous one; sides of the basal face gently converging backwards, with the posterior half bearing a short, carinate, triangular tooth. Declivous face laterally marked by a pair of longitudinal, convergent carinae.

Petiole and postpetiole cylindrical; anterior petiolar face truncate and dorsally carinate.

Gaster very narrow and elongate; the first segment ca. 1.5 times longer than broad.

Genitalia and subgenital plate as in Fig. 57.

Wings as in Fig. 58.

Sculpture. Head dorsum minutely reticulate and with sparse, irregular, thin rugosities; vertexal angles with irregular foveae; frons with very superficial foveae, small foveae. Ventral part of the head with the same type of sculpture as on the vertexal angles, the foveae diminishing in size and more superficial on the anterior part. Pronotum, mesonotum and scutellum reticulate and with sparse, irregular foveae; the same sculpture but separated by short, irregular rugosities on the basal face of the propodeum, on the anterior half of the petiole and on the sides of the postpetiole. Pedicel, pleurae, declivous face of the propodeum and first gastral tergite deeply reticulate; the reticulation less impressed and more shining on the remaining tergites, on the sternites and on the legs.

Pilosity. Body with three types of hairs: (1) suberect, long hairs, more dense on the head, on the mesosoma and on the apex of the gaster, sparse on the pedicel and on the legs, shorter on the first sternite; (2) short, sparse, appressed on the legs and on the gaster, rare on the pedicel; (3) similar to type (2) but longer, thicker and dense on the internal, anterior and posterior faces of the tibiae and on the tarsomeres.

Colour. Head, mesosoma and pedicel opaque black. Two anterior thirds of the first gastral tergite dark reddish brown. Remaining tergites, sternites and legs ferrugineous and slightly shining.

Measurements (in mm) and indices: TL 8.80; HL 1.36; HW 1.48; EL 0.51; PW 1.24; PeW 0.65; PpW 0.70; HBaL 1.16; HBaW 0.16; CI 108.8; PI 119.3; PPeI 190.8; PPpI 177.1; HBaI 13.8.

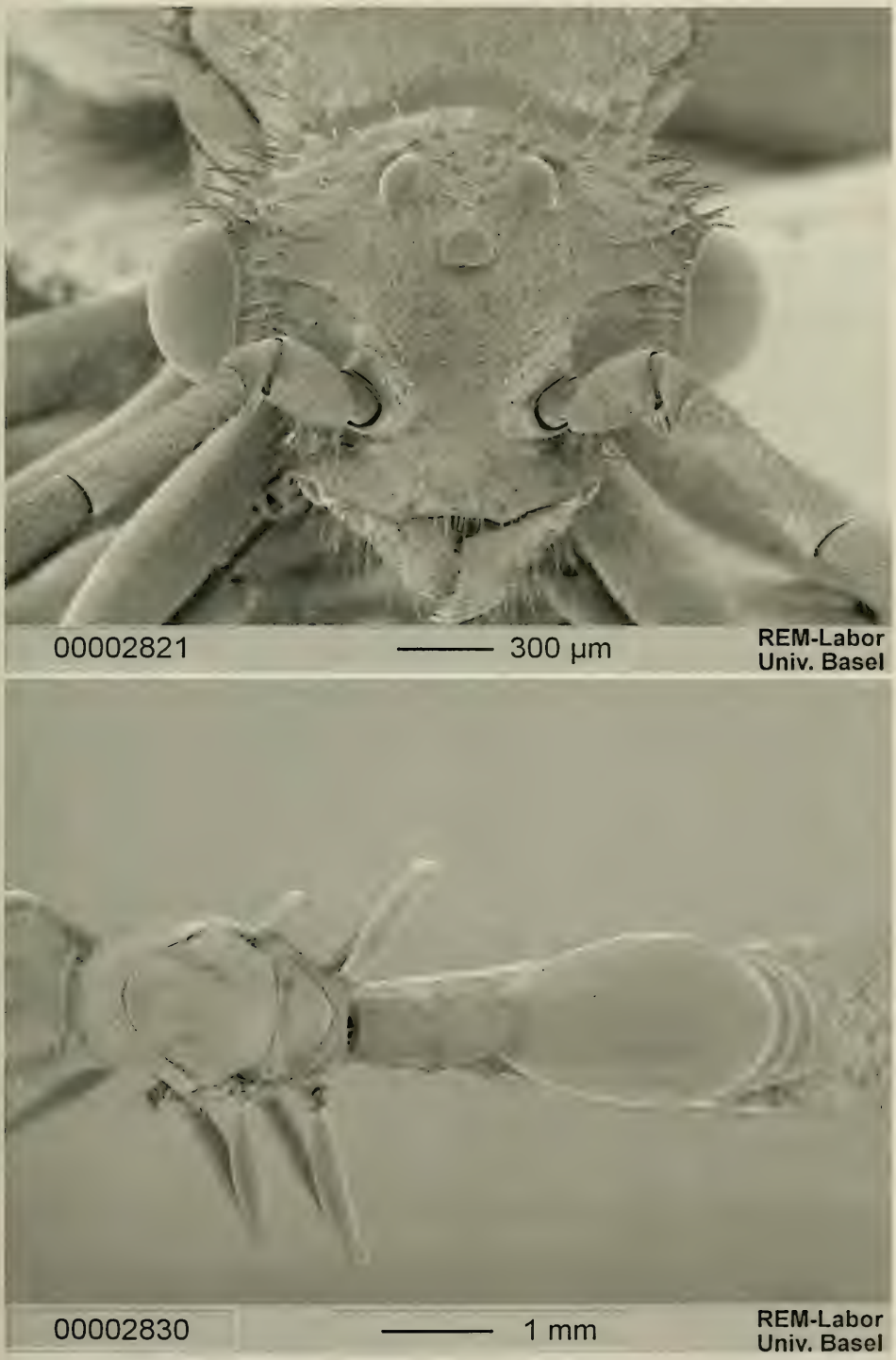


Fig. 56. *Cephalotes opacus* SANTSCHI. Male from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

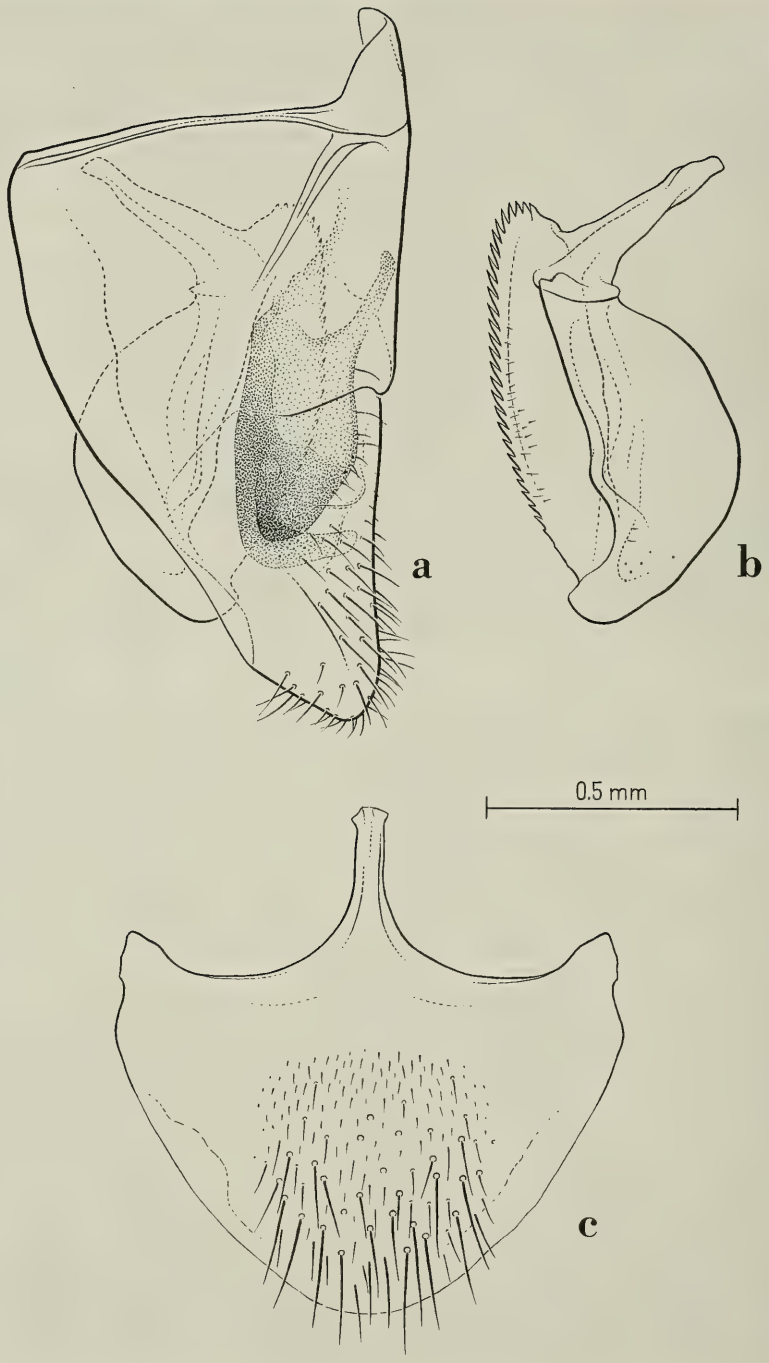


Fig. 57. *Cephalotes opacus* SANTSCHI. Male from Manaus, Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

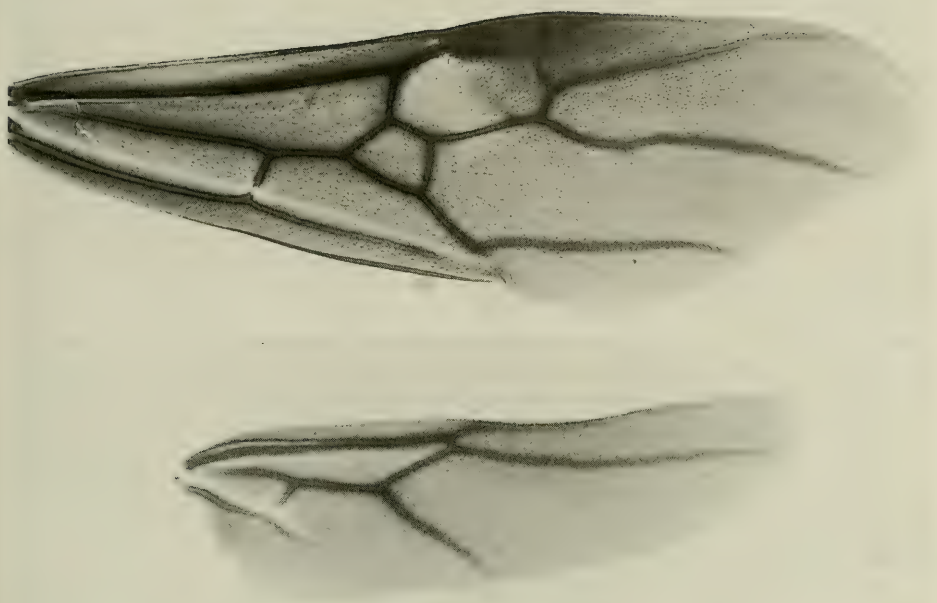


Fig. 58. *Cephalotes opacus* SANTSCHI. Male from Manaus, Brazil: fore and hind wings.

Material examined. - **Colombia**: Amazonas: La Chorrera, 30 km downhill Río Igara Paraná, 30.I–05.II.1974, 1 worker, 1 soldier, J. DESPLATS [MNHN]; Leticia, 03.XII.1973, 50 workers, 1 soldier, 1 gyne, M. CORN [MCZC].

Venezuela: Amazonas: Cerro de la Neblina, Base Camp 140 m, 0°50' N, 66°10'W, 10–20.II.1985, near Río Baria, 1 worker, P. J. & M. SPANGLER, R. FAITOUTE & W. STEINER [USNM].

Guyana: no further locality, 29.III, 03.IV.1901, 2 workers [USNM]. Essequibo: Kaietur, 06.VIII.1911, 1 worker, LUTZ [MCZC]; Oko R., Cuyuni trib. 25.VI.1936, 1 worker, N. A. WEBER [MCZC].

Surinam: Raleigh, Vallen-Voltzberg Res., Voltzberg Camp, 90 m, 29.I–13.II.1982, 1 worker, J. CARPENTER & D. TRAIL [MCZC]. Marowijne: Anapaike (Río Lawa), XI.1963, 2 workers, B. MALKIN [MZSP].

French Guyana: Saint Laurent Du Maroni: St. Jean Du Maroni, 1 worker (holotype) [NHMB].

Brazil: Amazonas: High Falls, Rio Tarumã, 30.8.1962, 1 worker, W. L. BROWN [MCZC]; Road BR–174, km 46, 11.II.1992, 4 workers [INPA]; Reserva Ducke, 26 km N of Manaus, 4.VIII.1982, 1 worker, A. Y. HARADA [INPA]; same locality, 22.I.1996, 2 workers, 1 male, M. L. DE ANDRADE [INPA]; Manaus, INPA, BR–174, km 70, II.1976, 1 worker, V. P. DANIEL [MZSP]; Novo Airão – Parque Nacional Jaú, Ig. Preguição, 1°59' S, 61°32' W, 26–29.VI.1994, 1 worker, A. QUINO. L. [INPA]. Pará: Serra Norte, Manganês, 12–15.IX.1985, 1 worker, W. FRANÇA [MPEG]; Benevides, Fazenda Morelândia,

20–23.IX.1991, 1 worker, W. FRANÇA [MPEG]; Tucuruí, I.1979, 1 worker, M. Alvarenga [MPEG]; Tucuruí, Rio Tocantins, 31.III–11.VI.1984, 2 workers [MPEG]; Mocambo, 5.XII.1977, 1 worker, M. F. TORRES [MPEG]; Rio Cuminá, 1 worker, SAMPAIO [MZSP]; Pirelli Plantation near Belém, 16.8.1962, 1 worker, P. F. DARLINGTON [MCZC]. Acre: Cruzeiro do Sul, 27.IX–19.X.1983, 1 worker, F. H. CAETANO [MZSP]. Rondônia: Ji-Paraná-Gleba, 25–28.II.1983, 2 workers J. ARIAS [MZSP]; Vilhena, XI.1973, 4 workers, M. ALVARENGA [MZSP]. Bahia: Barrolândia, 30.I.1994, 2 workers, F. P. BENTON [CPCC]; Una-Rébio, 30.I.1995, 1 worker, J. ASSIS & J. H. C. DELABIE [CPCC]. Espírito Santo: Linhares, IX.1972, 4 workers, M. ALVARENGA [MZSP]. Mato Grosso: Vila Vera, X.1973, 11 workers, M. ALVARENGA [MZSP].

Ecuador: Napo: Ecuador Oriente, 00°24' S, 76°36' W, Limoncocha, 14.XII.1967, resisted attack by *E . rapax*, 2 workers, C. W. & M. E. RETTENMEYER [MZSP]; San Pablo de Kantesiya, 14.XI.1998, 1 worker, J. M. TONZET [MHNG].

Peru: Callanga, 1 worker [MCZC]. Madre de Dios: Río Tambopata Res., 30 km SW Pto. Maldonado, 290 m, 12°50' S, 69°20' W, 16.III.1982, 7 workers, T. L. ERWIN et al. [MCZC]; Tambopata wild res. 12°51' S, 69°17' W, 290 m, 22–25.I.1985, 1 worker, J. CARPENTER & D. BOWERS [MCZC]; Cuzco Amazonico, 15 km NE of Puerto Maldonado, 19 & 26.VI.1991, 9 workers, 1 soldier, J. E. TOBIN & S. P. COVER [MCZC] .

Discussion. - The material we studied shows consistent differences between *opacus* and *placidus* in body sculpture and morphology of the propodeal spines (for other differences see under *placidus*). KEMPF (1959) synonymised the two without having seen the type of *opacus*. The worker from Orinoco (accompanied by a male) on which KEMPF (l. c.) based his synonymy is a typical *placidus* specimen and not *opacus*. *C. opacus* and *placidus* can coexist in narrow sympatry, which explains KEMPF's judgement to refer to only one species the two (heterospecific) Peruvian specimens from La Sombra he examined.

The presence or absence of gastral lamellae previously used to separate *abdominalis* from *opacus* is not consistent. We examined specimens from the same locality and probably originating from the same nest with gastral lamellae long, short or absent.

Among the material we studied the specimens from Venezuela, Guyana and most Brazilian specimens, except those from Espírito Santo, have generally short or no gastral lamellae, while longer lamellae are more frequent (but not unique) among Colombian and Peruvian specimens.

Distribution: Colombia, Venezuela, Guyanas, Surinam, Brazil, Ecuador, Peru, Bolivia.

Cephalotes placidus (SMITH)

Figs. 59, 60, 61

Cryptocerus placidus SMITH, 1860: 76. Male. Original description. Type locality: São Paulo de Olivença (Amazonas, Brazil). Type material: holotype male labelled: 1st label "St. Paulo Braz.", 2nd label "*Cryptocerus placidus* Smith", 3rd label "Coll. Smith 1829", 4th label (pink) "*Eucryptocerus placidus* (Sm.) Holotypus [added by Kempf], 5th label "*Eucryptocerus placidus* (Fr. Smith, 1860) det. W. W. Kempf", 6th label "Type Hym.: 1041 *Cryptocerus placidus* Smith Hope Dept. Oxford", in OXUM, examined. A second specimen in BMNH, labelled "*C. placidus*, type. Sm., Journ. Ent. I.76, 59 2", examined, is likely to belong to another species which we are unable to identify. We consider KEMPF's (1959) re-description of the Oxford specimen as a lectotype designation.

Cryptocerus fenestralis SMITH, 1867: 607. Gyne. Original description. Type locality: São Paulo de Olivença (Amazonas, Brazil). Type material: holotype gyne labelled "*Cryptocerus fenestralis*., (type) Smith, St. Paul, 70 16" in BMNH (KEMPF, 1963: 437), examined. Synonymy by KEMPF, 1964 a: 437.

Cephalotes placidus (SMITH), EMERY, 1922: 304. First combination in *Cephalotes*.
Eucryptocerus placidus (SMITH), KEMPF, 1959: 92, figs. 1, 4–7. Male. First combination in *Eucryptocerus*.
Eucryptocerus placidus (SMITH), SNELLING, 1966: 38, fig. 1. Gyne.

D i a g n o s i s . - A member of the *atratus* clade distinguishable from the other species, in the worker, for the following combination of characters: long, thick propodeal spines, deep foveolate sculpture and broad gastral lamella.

W o r k e r (Fig. 59). - Head subquadrate, less than one fourth broader than long. Border of the frontal carinae with a small denticle in the middle. Vertexal angles with two pairs of teeth; only the internal tooth with lamellaceous border and ca. twice larger than the external one.

Mesosoma. Anterior pronotal border with a superficial or without a notch in the middle. Pronotal dorsum with a pair of developed denticles. Propodeum with a pair of spines ca. 1.5 longer than the basal face.

Petiole subcylindrical, with truncate anterior face, unarmed and gently converging posteriorly. Postpetiole slightly higher than the petiole; anterior half of the postpetiolar sides broadly convex, in some specimens with truncate apex; posterior half converging posteriorly.

Gaster with a pair of broad lamellae narrowing at the apex.

Legs. Mid and hind femora without angle or denticle medially but with a pair of faint longitudinal carinae on the two posterior thirds. Mid and hind basitarsi long, slightly compressed laterally at the base; their diameter constant through the whole length.

Sculpture. Foveae on the mesosoma and pedicel much deeper than in *opacus* and *oculatus*.

Pilosity and colour. As in the other species of the clade.

Measurements (in mm) and indices: TL 8.04–8.80; HL 1.84–2.04; HW 2.24–2.48; EL 0.47–0.49; PW 2.44–2.56; PeW 0.60–0.70; PpW 0.70–0.83; HBaL 1.00–1.16; HBaW 0.23–0.27; CI 119.1–1224.0; PI 96.9–100.0; PPeI 365.7–380.0; PPpI 308.4–325.7; HBaI 23.0–23.3.

G y n e (Fig. 60) (description of SNELLING, 1966). - "Total length, 11.4 mm.; forewing, 10.9 mm; maximum head width, 3.0 mm; maximum head length (from anterior margin of lateral lobes), 2.9 mm; maximum thoracic width, 3.0 mm. Integument dull black, except the dark reddish-brown apical tarsal segments.

Head, excluding mandibles, very slightly longer than wide; mandibles strongly rugose; clypeus about as broad as long, triangular; frontal carinae slightly convergent anteriorly, margin of lower one-third slightly crenulate, with a few clavate setae occiput with a pair of low, pointed tubercles immediately above posterior ocelli; a low pointed tubercle on each side above eyes, with a similar tubercle immediately behind; front distinctly convex when viewed from above; occipital emargination rather deep; cheeks very broad, almost one-third as broad as head is long.

Pronotum nearly vertical anteriorly; humeral angles projecting forward as a narrow spine when viewed from above, pronotal crest strong laterally, absent medially, carinate, the carina raised on each side of median line as a pair of low humps, entire carina slightly crenulate; mesopleura with small spine above mid coxae; epinotum narrow, with a pair of spines directed caudad, the spines about as long as distance between their bases.

Petiole short, about twice as broad as long, anterior face vertical; postpetiole not swollen dorsally, only slightly swollen laterally; petiole and postpetiole without ventral projections; gaster more elongate than in worker, about one-third longer than broad, first tergite emarginate basally, disc with very fine striae which converge medially, anterior carina of first tergite distinct as far back as spiracle; remaining tergites discally roughened, all tergites with a narrow, dull, impunctate marginal band; first ventrite dull, sparsely punctate with a few irregular striae laterally; remaining ventrites roughened discally; all ventrites with narrow, impunctate apical margins which are slightly more shiny than those of tergites.

Integument generally dull, subopaque, mesoscutum, scutellum and abdomen somewhat shinier. Punctures of front moderate in size, separated by about a puncture diameter, becoming a little finer and sparser below, somewhat less distinct on pronotal lobes j punctures of

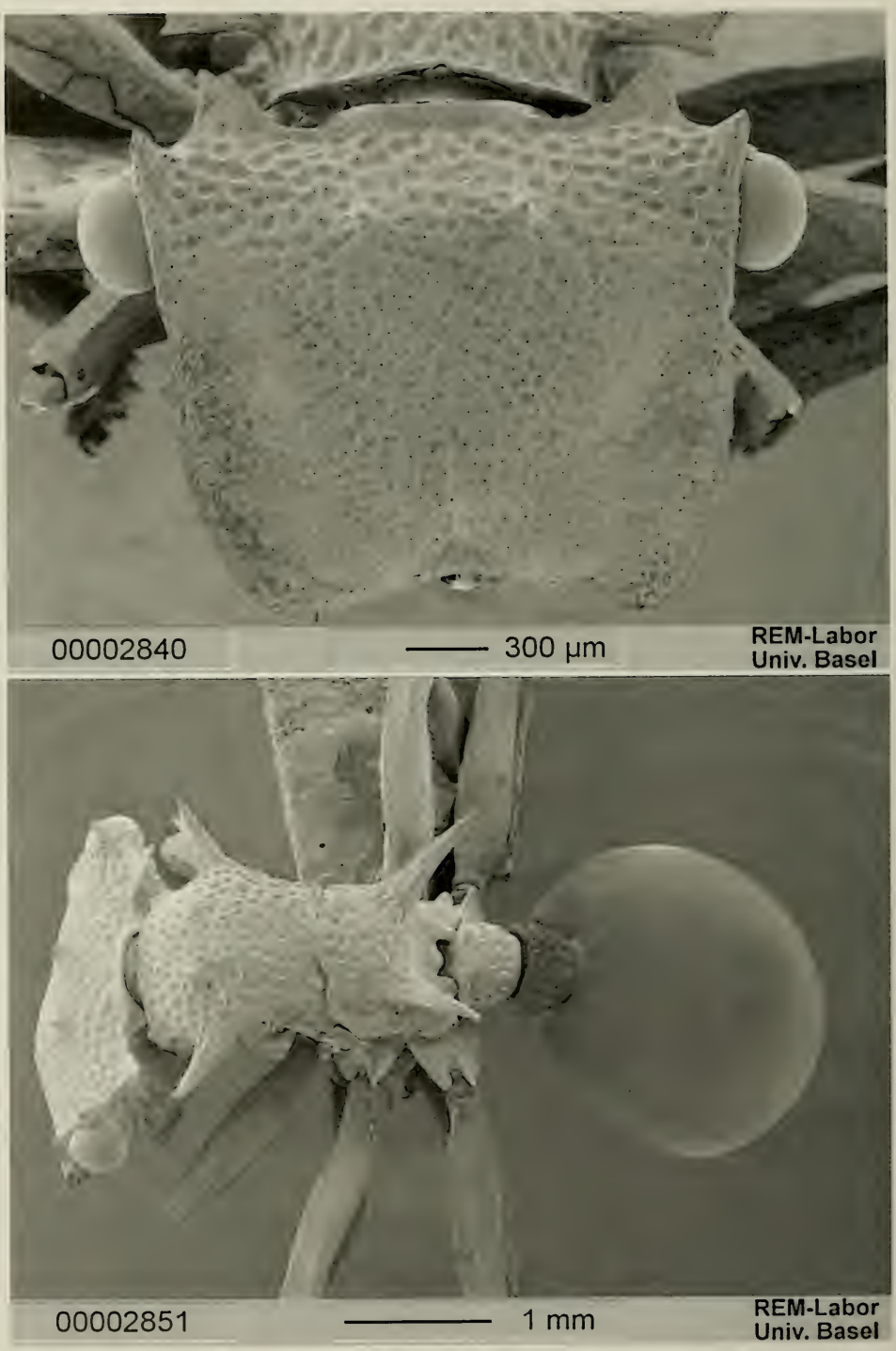


Fig. 59. *Cephalotes placidus* (SMITH). Worker from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

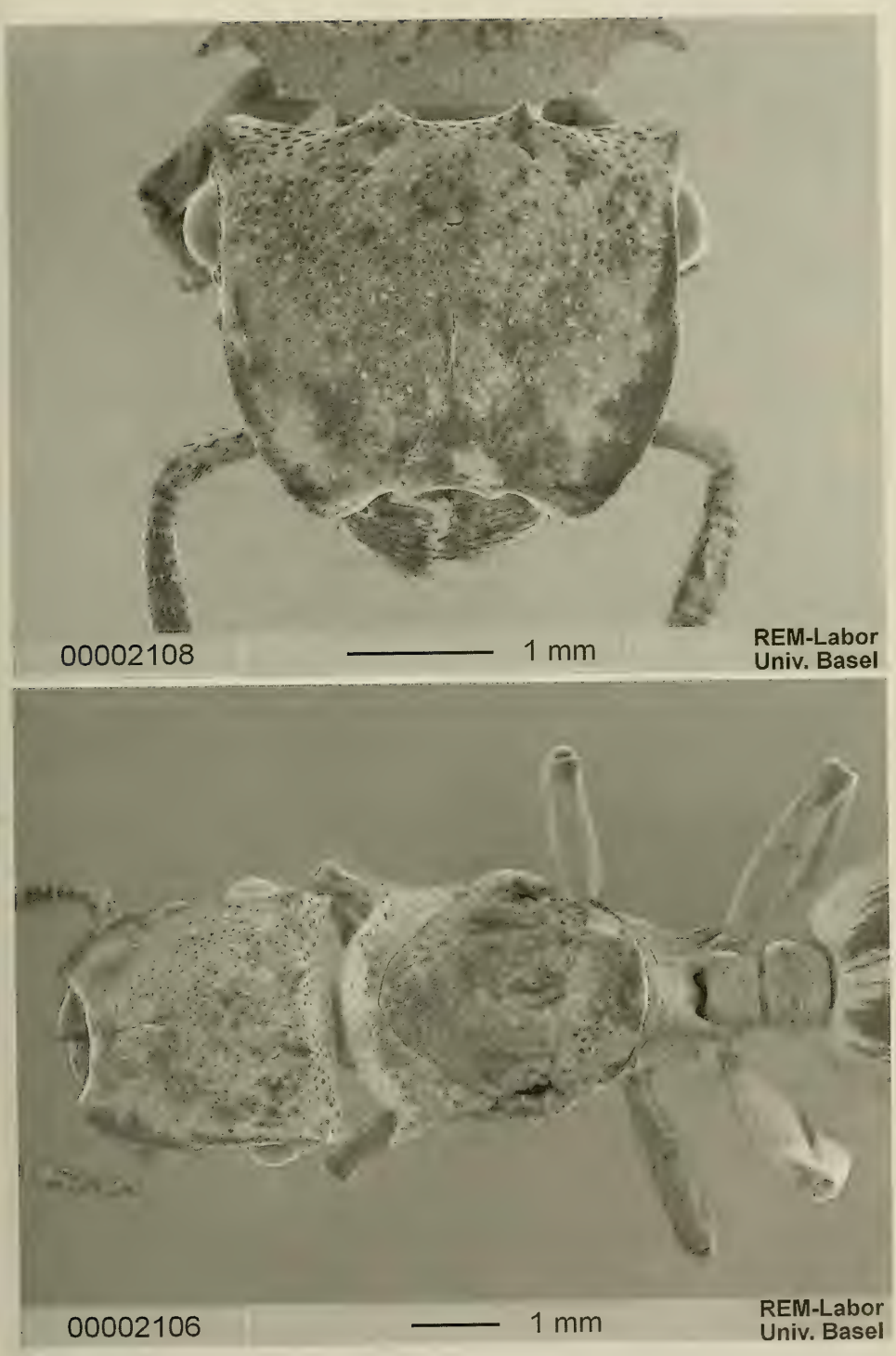


Fig. 60. *Cephalotes placidus* (SMITH). Gyne from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

occiput coarser than those of front, separated by a puncture diameter or less; cheeks rugoso-punctate; punctures of anterior and upper faces of pronotum equal to those of occiput, sparser medially, of lateral face coarse, rather close; punctures of mesoscutum slightly elongated, separated by a puncture diameter or less, becoming sparser and fainter laterad; those of disc about equal to those of occiput; punctures of upper mesopleural plate slightly finer than those of adjacent portion of pronotum, separated by slightly less than a puncture diameter; punctures of lower half of mesopleura, entire metapleura, lateral and posterior faces of epinotum obscure, scattered, the integument opaque, minutely granulose; punctures of scutellum slightly elongate, equal to those of mesoscutum, separated by a puncture diameter or less the integument slightly more shiny than elsewhere; punctures of basal face of epinotum coarse, deep, subcontiguous. Wings fuscous infuscate, except for clear submarginal cell; marginal cell closed and appendiculate apically, about 3.5 times as long as wide; submarginal cell about three-fourths as long as marginal; otherwise as figured by Kempf (1959:93) for the male."

Measurements (in mm) and indices: TL 12.86–13.70; HL 2.48–2.56; HW 3.00–3.12; EL 0.64; PW 3.04–3.20; PeW 0.92–1.00; PpW 1.08–1.10; HBaL 1.32; HBaW 0.32–0.34; CI 120.0–121.9; PI 97.5–98.7; PPeI 320.0–330.4; PPpI 281.5–291.0; HBaI 25.7.

Male (translation of the description of Kempf, 1959). - "Total length 9.7 mm; length of the cephalic capsule 1.45 mm; head width, including the eyes, 2.21 mm; length of the thorax 3.12 mm; length of the fore wing 7.6 mm. Black; funicular segments II – XII, legs, except the coxae, and gaster ferruginous. integument opaque, finely and densely punctuate; first gastral tergite, particularly in the center, and legs, particularly on the extensor face of the femora, with sculpture more superficial and slightly shining. Head with larger foveolae, superficial and sparse; with very short rugae disposed radially around the eyes; occiput rugose-reticulate. Pronotum, shield and scutellum with foveolae slightly larger but equally superficial and sparse. Basal face of the epinotum irregularly reticulate-rugose; declivous face with regular rugae, vertical and thinner. Dorsum and sides of the peduncular segments with fine, spaced, longitudinal rugae. Erect pilosity thick, yellowish, abundant on the body, nearly entirely lacking on the first gastral tergite and on the legs, excepted the flexor face of the femora and of the tibiae. Gaster with thin and short , sparse hairs, adherent to the integument. Pubescence more dense on the legs, very dense and very short on the funiculi.

Head transverse; interocular distance slightly larger than the length of the cephalic capsule. Clypeus considerably convex, with anterior face sloping and truncated in the middle, clearly separate from the superior face, the two forming a right angle, when seen in profile. Occipital angles with a triangular tooth large and projecting. Thoracic shoulders obtuse, not marked. Basal face of the epinotum with lateral borders converging behind, the triangular lobes of the posterior angle with pointed and sharp borders; postero-median impression without distinct margination in the middle. First tarsomere of the middle and hind legs slightly compressed, not remarkably enlarged. The two peduncular segments bear on each side a projecting tubercle, those of the petiole more ventral, not visible when seen from top. First gastral tergite 1 1/3 times longer than wide, the base superficially impressed in the middle of the articulation of the postpetiole.

Genitalia and subgenital plate as in Fig. 61.

Wings slightly darkened, with the venation dark-brown. Fore wing with black pterostigma, cubital cell nearly light and hyaline. Hind wing with venation originating from the anterior side of the radius, in the middle of the first abscissa, and with 9–10 hamuli."

Measurements (in mm) and indices: TL 7.72–9.40; HL 1.12–1.36; HW 1.48–1.76; EL 0.52–0.65; PW 1.28–1.60; PeW 0.56–0.72; PpW 0.64–0.80; HBaL 1.16–1.28; HBaW 0.16–0.20; CI 120.6–132.1; PI 102.8–119.3; PPeI 220.0–235.3; PPpI 193.7–222.2; HBaI 13.8–15.6.

Material examined. - **Colombia**: Amazonas: La Chorrera, 30 km downhill Río Igara Paraná , 23.I, 01–02.II, 05.II, 25.III.1974, 6 workers, 1 gyne, J. Desplats [MNHN]; Leticia, 24.II.1974, 2 workers, on *Helicornia* stems, A. Howden [MCZC].

Guyana: Berbice: Orinoco river, 2°42', 27.VII.1936, 1 worker, 1 male, N. A. Weber [MZSP].

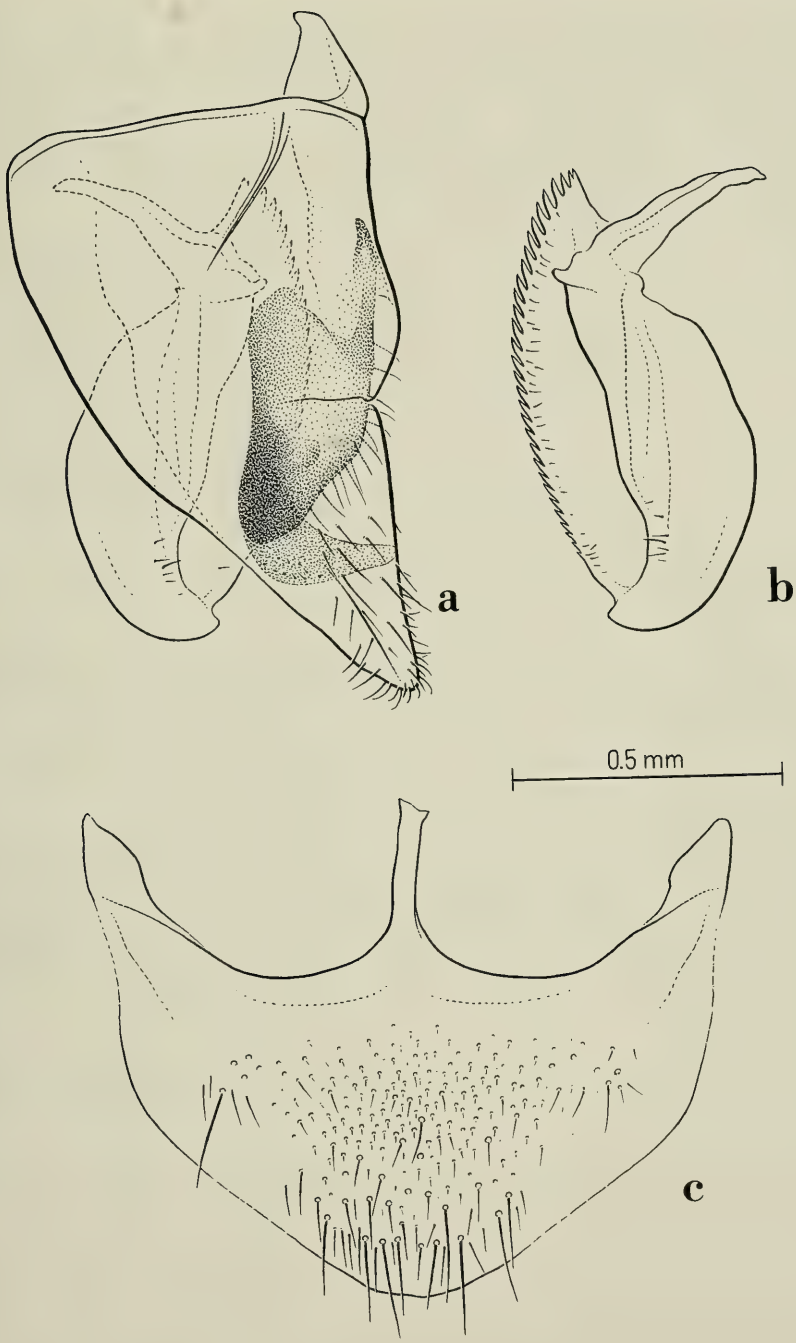


Fig. 61. *Cephalotes placidus* (SMITH). Male from Mato Grosso, Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Brazil: A m a p á : Rio Amazon, km 185, 9.V.1959, 1 worker, J. LANE [MZSP]; Amicohy, Braço Sul, 24.VI.1959, 2 workers, LANE & BICELLI [MZSP]. A m a z o n a s : no further locality, 1 worker, 1 gyne, 1 male, H. W. BATES [ZSMC]; St. Paul (= São Paulo de Olivença) 1 gyne (holotype of *fenestralis*) [BMNH], same locality, 1 male (holotype) [OXUM]; Reserva Fl. A. Ducke, 2°55' S, 59°59' W, 26.VIII.1982, 3 workers, ADIS et al. [CPCC]; same locality, 01–03.VIII.1981, 1 worker, J. RAFAEL [INPA]; same locality, 22–26.I.1996, 2 workers, 2 gynes, M. L. DE ANDRADE [INPA]; Manaus, BR–174, km 45 EEST, 17.VI.1994, 1 worker, C. OLIVEIRA [INPA]; Manaus, Res. Campina, BR–174, km 44, 02.VIII.1980, 1 worker [INPA]; Ponte Negra , Manaus, 5.III.1971, 1 worker [MZSP|. 20 km NE Manaus, on Caracaraí, 06.VI.1971, 1 worker, W. L. & D. E. BROWN [MCZC]; Rio Unini, Lago Pedras, 22.XI.95, BINDÁ & ALENCAR, 3 workers [INPA]; Rio Autaz, 1 worker, ROMAN [MCZC]; Benjamin Constant & vicinity, 19.IX.1962, 14 workers, 1 gyne [MCZC, MZSP]; same locality, 18–28.IX.1962, 43 workers, 1 gyne, K. LENKO [MCZC, MZSP]; Ig. Marianil, Rio Branco Rd. 24 km NE of Manaus, 26.VIII & 09.IX.1962, 3 workers, W. L. BROWN [MCZC, MZSP]. P a r á : Serra Norte, R. Salobo, 21.IX.1985, 1 worker, M. ZANUTO [MPEG]; same locality, Manganês, 24.VI.1986, 1 worker, J. DIAS [MPEG]; Jacareacanga, X.1959, 1 worker, M. ALVARENGA [MZSP]. A c r e : Rio Branco, 25.X–8.XI.1991, 2 workers, F. F. RAMOS et al. [MPEG]. R o n d ô n i a : Ouro Preto do Oeste, 25–28.III. 6.IV.1985, 19 workers, F. F. RAMOS & W. FRANÇA [MPEG]; Vilhena, XI.1973, 5 workers, M. ALVARENGA [MZSP]. M a t o G r o s s o : Vila Vera, X.1973, 1 worker, M. ALVARENGA [MZSP]; Sinop , 55°37' W, 12°31' S, X.1974, 21 workers, 3 males, ALVARENGA [MZSP].

Peru: La Sombra, 22.VIII.1920, 1 worker, Cornell Univ. exp. [MZSP]. L o r e t o : Pucallpa, 200 m, 11–20 XI.1964, 2 workers, J. SCHUNKE [MCZC]; same locality, 15.IV.1965, 15 workers, J. SCHUNKE [MZSP].

D i s c u s s i o n . - KEMPF (1951) decided the synonymy of *placidus* with *opacus* on the examination of three workers, each on a separate pin, two from La Sombra, Peru, and one from Brazil. KEMPF's (l. c.) description of *opacus* is based on the worker from Brazil and on the smaller specimen from Peru which must be referred to *placidus*. The second worker from Peru is *opacus*. Later KEMPF (1959) examined the type of *placidus* (a male) and compared it with a male associated with a worker from the Orinoco River he identified as *opacus* but was again a true *placidus*. We had the opportunity to study part of the material examined by KEMPF and the synonymy of *opacus* and *placidus* cannot be maintained. The workers of *placidus* can be immediately distinguished from those of *opacus* for the heavier body sculpture, for the longer propodeal spines and for the greater HBaI and the analogously computed mid basitarsal Index (MBaI) values as follows:

	HBaI	MBaI
placidus	23.0–23.3	31.2–32.9
oculatus	19.2–20.6	25.0–28.6

The gyne and the male of *placidus* also have much stronger body sculpture and longer propodeal spines than the one of *opacus*.

The synonymy of *fenestralis* (based on a gyne) with *placidus* (described on males), proposed by KEMPF (1963) is further confirmed by the study of gynes associated with workers and males associated with morphologically identical workers as listed under the material examined.

FERNÁNDEZ & PALACIO (1995) and FERNÁNDEZ et al. (1996) report this species from the Colombian states of Meta, Vichada and Caquetá.

D i s t r i b u t i o n : Colombia, Guyana, Brazil, Peru.

5.6.3. The *pusillus* clade

The two species constituting this clade, *pusillus* and *columbicus*, have been considered as only one (*pusillus*) by KEMPF (1951). *Pusillus* was regarded by KEMPF (l. c.) as a member of his "*spinosus* species group" which is roughly equivalent to our *laminatus* clade and with which it shares several characters. In our analysis *pusillus* and *columbicus* result separate and paraphyletic respect to the *laminatus* clade. The main reason for this is the presence of fine reticulation under the head, a character present in *solidus* and in all the members of the *laminatus* clade but absent in *pusillus* and *columbicus*. Another character separating *pusillus* and *columbicus* from the members of the *laminatus* clade (absence of angulate femora in the former vs. presence in the latter) is actually present only in the basal species of the *laminatus* clade and absent in the internal ones. The synapomorphies of the *pusillus* clade resulting from our phylogenetic reconstruction are the following:

1. Frontal carinae of the soldier not reaching the vertex. This character is present also in some ingroup species of the *laminatus* clade.
2. Aedeagus with long spines hidden by the basal projection (see Figs. 67, 69).
3. Internal face of the aedeagus ventrally concave (see Figs. 67, 69).

We are inclined to recognise a significant phylogenetic value to characters 2 and 3. The crucial fact forcing the distinction between the *pusillus* clade and the *laminatus* clade, however, is the position of the insufficiently known species *solidus* (q. v.) – intermediate between the two clades in our *Cephalotes* phylogeny. This position may be subject to change after discovery of the *solidus* soldier, gyne and male.

Species included in the clade: *columbicus*, *pusillus*.

Cephalotes columbicus (FOREL) new combination and new status

Figs. 62, 63, 64, 65, 66, 67

Cryptocerus pusillus var. *columbica* FOREL, 1912: 201. Worker, soldier. Original description. Type locality: Magdalena (Santa Marta, Colombia). Type material: 19 workers, 12 soldiers labelled "Santa Marta, Colombie", Forel, in MHNG, 1 worker in NHMB, examined.

Paracryptocerus pusillus columbicus (FOREL), KEMPF, 1951: 183. First combination in *Paracryptocerus*.

Zacryptocerus pusillus columbicus (FOREL), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *pusillus* clade characterised in the worker and soldier by the more regular body foveae and by the broad, transparent, gastral lamellae.

W o r k e r (Fig. 62) (description of KEMPF, 1951). - "Length 5.5 mm. Median head length 1.36 mm; interocular width 1.68 mm; Weber's length of thorax 1.58 mm. Black; the following dark reddish brown: frontal carinae, apical three tarsal segments, apex of posterior epinotal spines; anterolateral lamellate border of gaster. Very similar to the typical *pusillus*, from which it differs by the following peculiarities:

Scales on upper surface of head minute to obsolete, especially on the anterior half. Foveolae limited to narrow band in front of the occipital border. Outer face of fore coxae distinctly striated. Foveolae on upper surface of thorax well separated by finely reticulate-punctate, flat, opaque interstices. First pronotal tooth spine-like and prominent, the second tooth rather obsolete. First epinotal tooth comparatively small, the posterior spine very long and slender; as measured from the posterior rim of the spiracle to the tip, longer than 1/3 of the maximum length of the thorax. Petiole without a lateral tooth. Scales of gaster minute, obsolete abovediscad. Integument opaque."

Fig. 62. *Cephalotes columbicus* (FOREL). Worker from Altagracía de Orituco, Venezuela: head (top) and meso- and metasoma (bottom) in dorsal view.

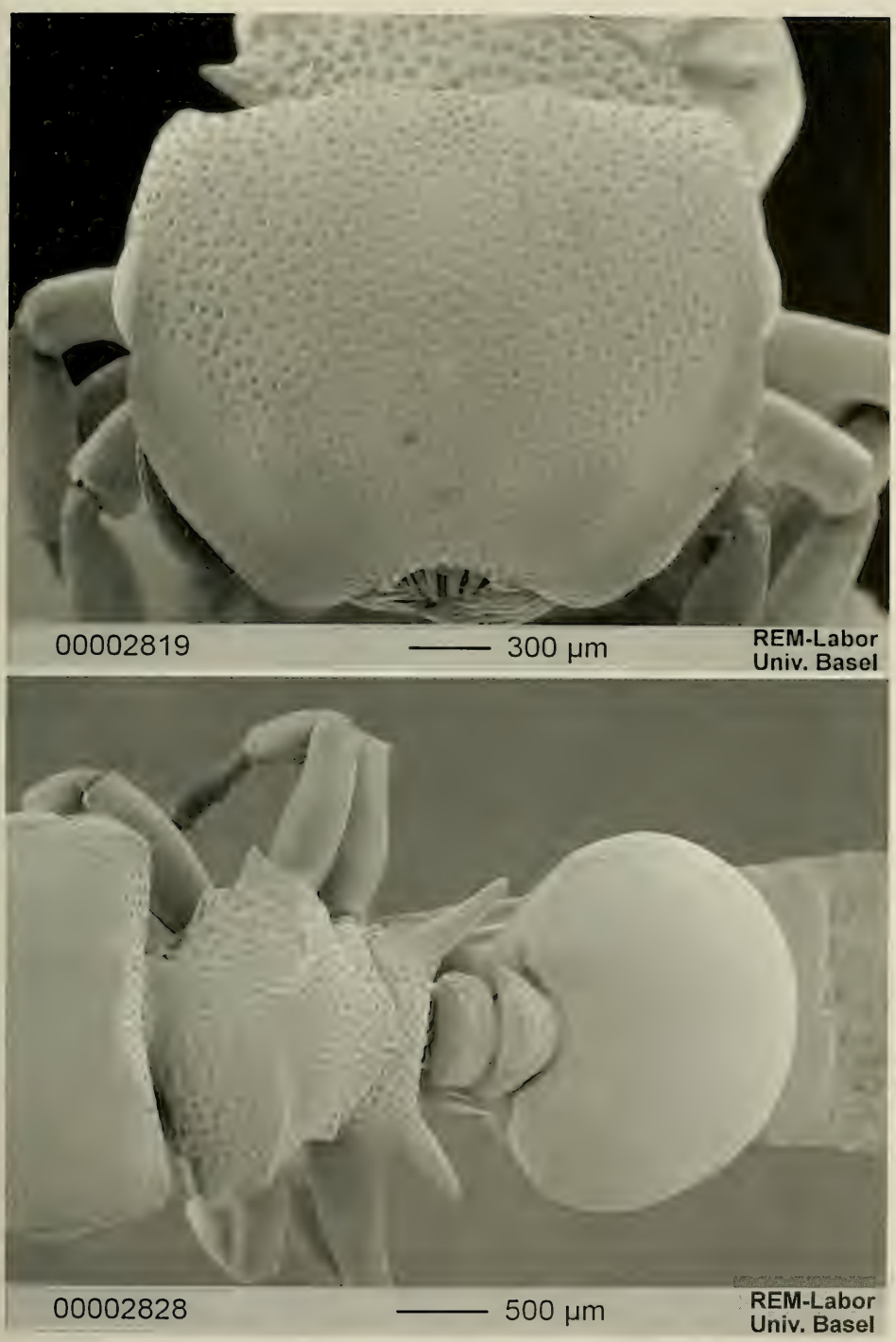


Fig. 63. *Cephalotes columbicus* (FOREL). Soldier from Puerto Colombia, Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 64. *Cephalotes columbicus* (FOREL). Gyne from Hato Masaguaral (Guarico), Venezuela: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 5.18–5.76; HL 1.22–1.36; HW 1.68–1.88; EL 0.36–0.39; PW 1.32–1.54; PeW 0.51–0.60; PpW 0.58–0.68; HBaL 0.62–0.67; HBaW 0.13–0.16; CI 137.7–138.2; PI 122.1–127.3; PPeI 256.7–258.8; PPpI 226.5–227.6; HBaI 21.0–23.9.

S o l d i e r (Fig. 63). - Head broader than long and gently convex dorsally. Frontal carinae convex, converging posteriorly and terminating over the posterior border of the eyes. Vertexal angles truncate. Vertex with a pair of median, broad denticles. Mandibles broad, with the sides neither angulate nor denticulate.

Mesosoma. Scapular angles well visible in dorsal view. Humeral angles with a triangular tooth followed by another shorter and round denticle; pronotum converging posteriorly. Pronotal carina broadly interrupted in the middle. Promesonotal suture impressed. Sides of the mesonotum with a pair of small, pointed denticles. Propodeal suture deeply impressed. Propodeum with clearly differentiate basal and declivous faces; basal face with two pairs of lateral projections, the anterior one, minutely denticulate, pointed or obtuse, the posterior pair long, spiniform, thick and pointed.

Petiole with the anterior face truncate; its sides unarmed or with a pair of minute denticles. Postpetiole broader than the petiole and with convex dorsum; postpetiolar sides with a pair of round or subpointed teeth, originating on the anterior face and pointing outwards.

Gaster oval, with a broad lamella not surpassing the stigma posteriorly.

Legs. Fore coxae protruding anteriorly. Mid and hind femora dorsally neither angulate nor denticulate. Mid and hind basitarsi not flat and without broad base.

Sculpture. Head deeply and irregularly foveolate; the foveae denser and deeper on the vertexal angles and absent on the frontal carinae. A microscopic reticulation fills the interfoveal spaces and the frontal carinae. Ventral face of the head, propleurae and pronotum similarly sculptured but the foveae are denser, larger and deeper. Mesonotum sculptured as the vertexal angles. Basal face of the propodeum with dense, almost contiguous, round and oval foveae superimposed by reticulation. Declivous face of the propodeum simply reticulate and with longitudinal rugosities on the sides. Meso- and metapleurae reticulate and with sparse, superficial, oval foveae. Pedicel reticulate and with dense, superficial, irregular foveae. Gaster and legs reticulate. Outer face of the fore coxae with superficial longitudinal rugosities on the posterior half. Anterior fourth of the first gastral tergite with superficial, oval foveae. Centre of the posterior half of the first gastral sternite shining. Outer face of tibiae irregularly foveolate.

Pilosity. Each fovea bears a minute appressed hair. Other body surface without foveae with appressed, sparse, thin, short hairs. Posterior border of the gastral segments and legs with sparse clavate hairs. Gastral sternites with suberect, long, pointed hairs.

Colour. Black. Frontal carinae and gastral lamellae ferrugineous, tarsomeres darker.

Measurements (in mm) and indices: TL 6.88–7.28; HL 1.72–1.80; HW 2.32–2.40; EL 0.44–0.45; PW 2.08–2.10; PeW 0.68–0.66; PpW 0.73–0.76; HBaL 0.68–0.72; HBaW 0.18–0.19; CI 133.3–134.9; PI 111.5–114.3; PPeI 305.9–318.2; PPpI 276.3–284.9; HBaI 26.4–26.5.

G y n e (Fig. 64) (previously undescribed). - Head strongly convex dorsally. Frontal carinae convex anteriorly; their sides converging in front of and ending before the posterior border of the eyes. Vertexal angles nearly round. Vertex with a pair of low median swellings. Mandibles as in the soldier.

Mesosoma. Humeral angles with a pointed anterior tooth. Pronotal carina narrow, superficially interrupt in the middle, poorly marked on the sides. Mesonotum and scutellum flat. Lower mesopleura with a broad, round denticle. Basal face of propodeum with a pair of thick teeth with round or pointed apex and slightly diverging; declivous face, posteriorly, with converging sides.

Petiole with the anterior face oblique, posterior face short and declivous posteriorly; petiolar sides convex, unarmed or armed with a pair of minute denticles. Postpetiole broadly convex; anterior sides of the postpetiole with a broad, obtuse expansions or unarmed.

Gaster protruding anteriorly and with a margination not surpassing the stigma posteriorly.

Legs. Fore coxae with an anterior lobe. Mid and hind femora not angulate. Mid and hind basitarsi not flat and not broad at the base.

Wings as in Fig. 65.

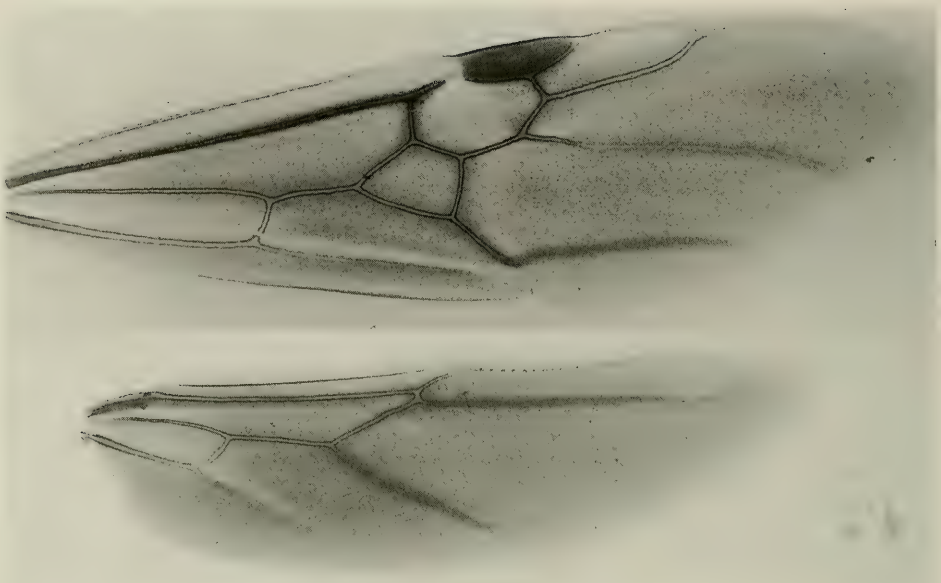


Fig. 65. *Cephalotes columbicus* (FOREL). Gyne from Altagracía de Orituco, Venezuela, fore and hind wings.

Sculpture. Head covered with small foveae sometimes as broad as their interspaces, denser on the vertexal angles and minutely reticulate. Frontal carinae minutely reticulate and without foveae. Ventral part of the head superficially shining and with dense, deep foveae. Pronotum and propleurae reticulate and with dense, deep foveae. Upper and anterior half of the lower mesopleurae, dorsal third of the metapleurae, basal face of the propodeum, posterior face of the petiole and postpetiole reticulate and with dense, small, slightly irregular foveae. Mesonotum superficially shining and with variably clumped foveae separated by longitudinal, irregular rugosities. Scutellum with sculpture similar to the one of the mesonotum but denser. Anterior face of the petiole, posterior half of the lower mesopleurae, remaining metapleurae, gastral tergites and legs reticulate. Anterior fourth of the first gastral tergite with small foveae more superficial posteriorly. Outer face of the tibiae with minute, irregular foveae. Gastral sternites superficially reticulate on the sides and shining in the middle.

Pilosity. Each fovea bears a minute appressed hair. Other surfaces without foveae with short, appressed, sparse, thin hairs. Mesosoma, pedicel and gaster with slightly clavate, subdecumbent hairs, denser on the sternites. Gastral sternites with additional sparse, suberect, long, pointed hairs.

Colour. Black. Frontal carinae dark ferrugineous.

Measurements (in mm) and indices: TL 11.04–11.93; HL 1.92–2.06; HW 2.32–2.54; EL 0.48–0.52; PW 2.16–2.52; PeW 0.83–0.96; PpW 1.04–1.20; HBaL 0.78–0.79; HBaW 0.20–0.22; CI 117.6–123.3; PI 100.0–107.4; PPeI 260.2–262.5; PPpI 200.0–210.0; HBaI 25.3–28.2.

M a l e (Fig. 66) (previously undescribed). - Head (eyes included) more than 1/3 broader than long; sides of the head convex and converging posteriorly. Vertex dorsally protruding, bearing salient ocelli. Compound eyes broadly convex, in the middle of the sides of the head. Frontal carinae diverging backwards, not reaching the median ocellus posteriorly. Frons flat. Clypeus convex.

Mandibles not carinate. Scapes thick, twice as long as the first funicular joint; remaining funicular joints filiform and thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards, without carinae. Mesonotal scutum convex in side view; median Mayrian furrow little impressed. Scutellum

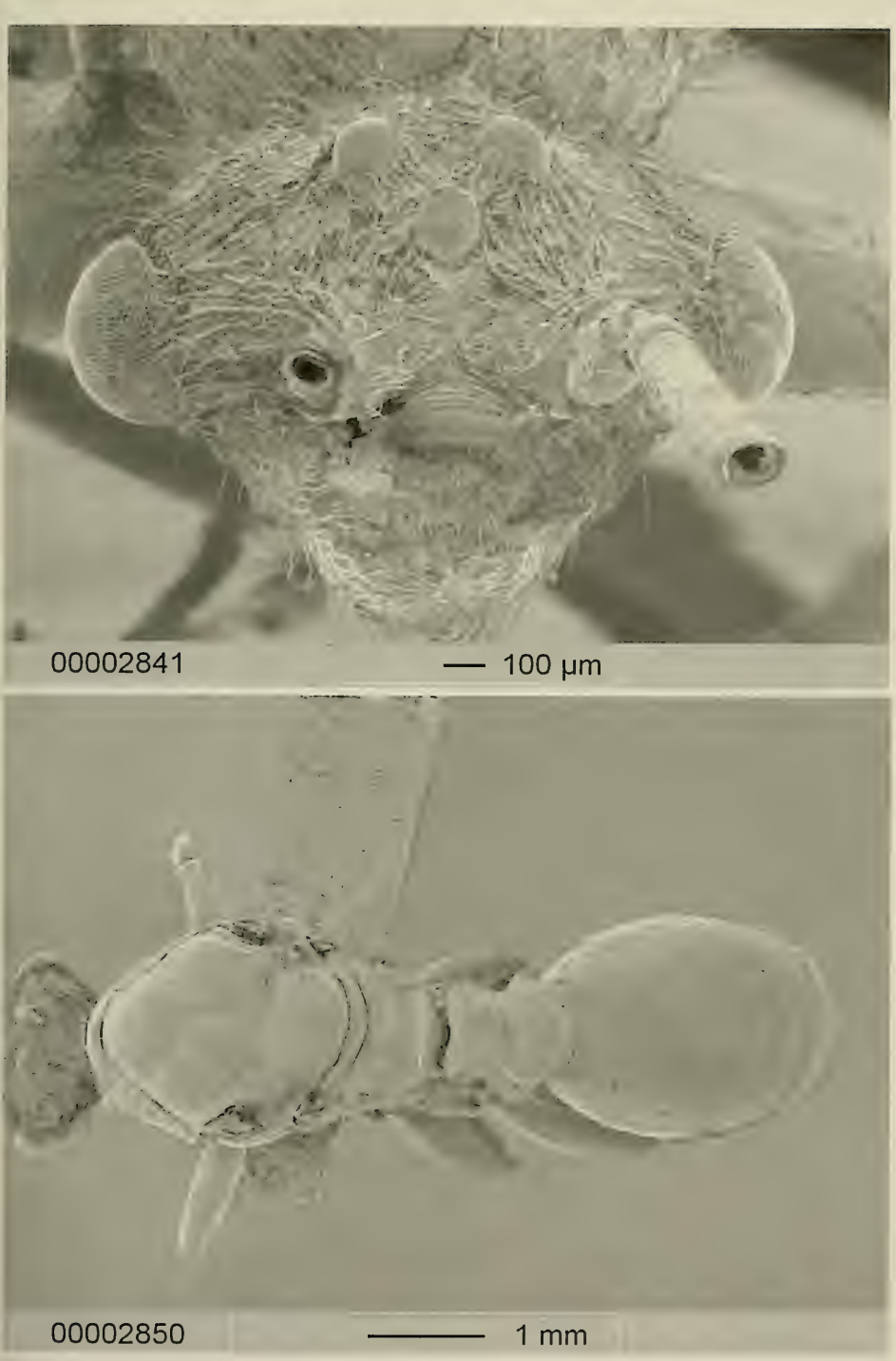


Fig. 66. *Cephalotes columbicus* (FOREL). Male from Altagracía de Orituco, Venezuela: head (top) and meso- and metasoma (bottom) in dorsal view.

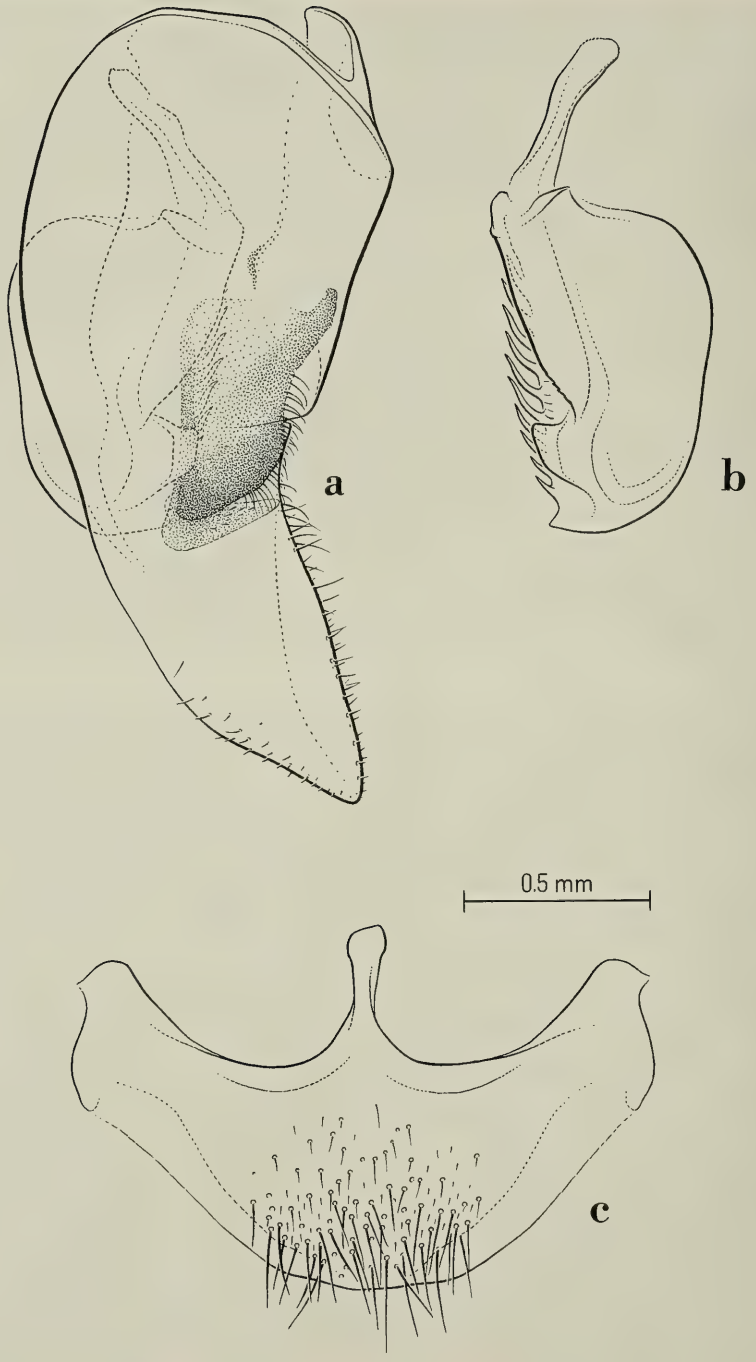


Fig. 67. *Cephalotes columbicus* (FOREL). Male from Altagracía de Orituco, Venezuela. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

convex, its sides gently converging posteriorly. Propodeum with differentiate basal and declivous faces; basal face gently convex; declivous face shorter than the basal one and almost straight. Propodeal sides divides from the dorsal face by a longitudinal carina.

Petiole with concave anterior face, superior face, flat and convex posteriorly; petiolar sides unarmed or with a pair of small denticles medially. Postpetiole convex dorsally; its sides with a pointed denticle.

Gaster as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 67.

Wings. As in the gyne.

Sculpture. Head dorsum irregularly rugulose and punctate; both structures are superimposed to irregular foveae on the vertexal angles and on the ventral face of the head. Ventral part of the head around the eyes with transversal rugosities. Mesosoma and peduncular segments reticulate and with very superficial, irregular foveae and thin longitudinal rugosities, the foveae absent on the declivous face of the propodeum and on the metapleurae; the reticulation stronger on the pedicel. First gastral tergite strongly reticulate and slightly granulose laterally in some specimens; this same type of sculpture but more superficial on the remaining tergites and on the sternites. Legs superficially reticulate and slightly shining. Outer face of the fore femora with faint, longitudinal rugulations.

Pilosity. Body with dark yellow, long, flexuous, thin, pointed hairs, dense on the head, on the mesosoma, on the pedicel and on the gaster, sparser on the legs. Legs with additional similar hairs but appressed, thinner and shorter.

Colour. Black. Coxae, two proximal thirds of the femora, and tarsi brown. Distal third of the femora and of the tibiae yellow.

Measurements (in mm) and indices: Measurements (in mm) and indices: TL 8.28–8.40; HL 1.08; HW 1.44; EL 0.49–0.52; PW 1.48–1.56; PeW 0.86–0.87; PpW 1.00–1.04; HBaL 0.88; HBaW 0.14–0.15; CI 133.3; PI 93.6–97.3; PPeI 172.1–179.3; PPpI 148.0–150.0; HBaI 15.9–17.0.

Material examined. - **Colombia**: Magdalena: Santa Marta, 20 workers, 12 soldiers (type series), FOREL [MHNG, NHMB]; Río Frío, 10.IV.1916, 1 worker, DARLINGTON [MCZC]; same locality, 2 workers, March 1924, W. M. MANN [MZSP]; Donjaca, 10 workers, S. A. G. SALT [MCZC]; Ciénaga, 2.6.1927, 3 workers, G. SALT [MCZC]. Atlántico: Puerto Colombia, 2 soldiers, A. H. STURTEVANT [USNM].

Venezuela: no further locality, 1 worker [NHMB]; no further locality, 1 worker, 4 soldiers [MNHN]. Sucre: Parque Nacional Mochima, 15 m, 2.X.1986, 2 workers, CANCELLO & BRANDÃO [MZSP]. Anzoátegui: 9 km south of Clarines, 2.XI.1986, 1 worker, Cancello, Lattke & Brandão [MZSP]. Delta Amacuro: Orinoco Delta, I-II.1935, 1 gyne, N. A. WEBER [MCZC]. Zulia: Maracaibo, 1902, 1 worker, E. POIRIER [NHMB]. Guarico: Hato Masaguaral, 44 km S Calabozo, 11–19.V.1985, 1 gyne, MENKE & CARPENTER [USNM]; La Cruz-Ruviera, 1925, 1 worker, M. GRISOL [MNHN]; Altagracía de Orituco, 17.III.1982, 38 workers, 6 soldiers, 1 gyne, 3 males, C. R. F. BRANDÃO & L. O. CAMPOS [MZSP]. Cojedes: Merecure, 2 km NE Piñero, near El Baúl, 22–24.X.1986, 1 worker, CANCELLO & BRANDÃO [MZSP].

Discussion. - The worker, soldier, gyne and male of *C. columbicus* can be distinguished from those of *pusillus* by the shallower, more rounded foveae. In addition *columbicus* differs from *pusillus* in the worker and in the soldier by the broader lamellae of the vertex and of the gaster, in the gyne by the broader head and higher PPeI and, in the male, by higher CI and by the scutellum not strongly narrowing posteriorly. Since these characters result constant within the abundant material of *pusillus* and *columbicus* we examined, and *pusillus* and *columbicus* are likely to be sympatric at least in areas of Colombia and Venezuela, the latter must be regarded as a valid species.

Distribution: Colombia, Venezuela.

Cephalotes pusillus (KLUG) new combination

Figs. 68, 69, 70, 364, 365, 366

Cryptocerus pusillus KLUG, 1824: 202. Worker. Original description. Type locality: South America. Type material: Syntype workers presumably in the Museum für Naturkunde der Humboldt-Universität Berlin (ROGER, 1862: 297), and in the Museo regionale di Scienze Naturali, Torino (CASOLARI & CASOLARI MORENO, 1980: 84) (not available for the present study).

Cryptocerus elongatus KLUG, 1824: 214. Gyne. Original description. Type locality: South America. Type material: a gyne presumably in the Museum für Naturkunde der Humboldt-Universität Berlin (ROGER, 1862: 297) (not available for the present study). Synonymy by ROGER, 1862: 297.

Formica caustica KOLLAR, 1832, in POHL & KOLLAR, 1832: 115, fig. 12. Worker. Original description. Type locality: Brazil. Type material not available for the present study. Synonymy by DE DALLA TORRE, 1893: 143. Note: synonym of *minutus* in EMERY (1890) and FOREL (1895).

Cryptocerus obtusus SMITH, 1858: 191. Soldier. Original description. Type locality: Santarem (Brazil). Type material: a syntype worker labelled "Santarem, 54 63, 174, *C. obtusus* (type) Sm.", other label (probably more recent): "*pusillus*, Rio", examined; a syntype worker labelled "Amazonas, H. W. Bates" in the ZSMC (FOREL, 1911 b: 262), examined. Synonymy by FOREL, 1911 b: 262.

Cryptocerus obtusus KLUG, EMERY, 1896: 636. Male.

Cryptocerus pusillus var. *brevispinosa* SANTSCHI, 1921 b: 127, fig. 2C. Worker. Original description. Type localities: S. Ignacio, Villa Lutecia, Cerro Cora in the govern. of Misiones, Córdoba (Argentina), Paraguay, Alto da Boa Vista (Rio de Janeiro, Brazil). Type material: 3 syntype workers from Córdoba, Misiones and Paraguay in NHMB (examined). Synonymy by KEMPF, 1951: 176.

Cryptocerus pusillus KLUG, EIDMANN, 1936, pl. 1 fig. I 11. Egg.

Paracryptocerus pusillus (KLUG), KEMPF, 1951: 176, figs. 118, 121. Worker, soldier, gyne. First combination in *Paracryptocerus*.

Paracryptocerus pusillus (KLUG), WHEELER & WHEELER, 1954 b: 156, fig. 41. Larva.

Paracryptocerus pusillus (KLUG), KEMPF, 1956: 102, figs. 1–13. Male genitalia.

Zacryptocerus pusillus, OLIVEIRA & SAZIMA, 1984: 145. First combination in *Zacryptocerus*.

Zacryptocerus pusillus (KLUG), OLIVEIRA, 1986: 307, fig. 12. Worker.

D i a g n o s i s . - A member of the *pusillus* clade characterised in the worker and soldier by the less regular body foveae and by the narrow, semi-transparent gastral lamellae.

W o r k e r (Fig. 366) (description of KEMPF, 1951). - "Length 4.4 mm. Median head length 1.14 mm; Weber's length of thorax 1.29 mm. Black; the following ferruginous: apex of mandibles, anterior portion of frontal carinae, apex of last funicular segment, apex of femora and basitarsi, distal half of the following tarsal segments, anterolateral border of first gastral tergite, apex of lateral projections of peduncular segments.

Head subopaque, about as long as broad; interocular distance subequal to maximum length of head (57:58). Sides of head subparallel, posterior margin between the internal corners of the short, obliquely truncate, infuscated occipital lamellae evenly curved and emarginate. Apical border of occipital lamellae straight. Cheeks strongly marginate beneath, densely covered with flat, silvery hairs, which lie in grooves on the posterior portion of the vertex. Eyes small, their maximum diameter less than 1/3 of the median head length.

Thorax opaque. Anterior border arcuate, shoulders angulate. Pronotum somewhat expanded laterally behind into a narrow, denticulate crest, with two short teeth on each side, the posterior tooth distinctly shorter than the anterior; posterior corner of pronotum rectangular and projecting. Promesonotal suture distinct. Mesonotum on each side with a very small, subrectangular tooth. Mesoepinotal suture vestigial, obsolete mesad. Basal face of epinotum in the same plane as mesonotum, transverse, very short, with a short lateral tooth, longer than the second pronotal tooth, and a very long, subcylindrical posterior spine arising from the

posterior corner, diverging about 45° degrees from the longitudinal axis. Dorsum of thorax moderately both longitudinally and transversely convex. Declivous face not excavate mesad, nor crested laterad. The entire thorax finely reticulate-punctate, with rather dense, sharply impressed, more or less elongate foveolae, each containing an appressed silvery, elongate glistening scale. Declivous face without nacrosculpture and without scales. Laterotergite of pronotum and mesopleura more or less regularly rugose and sparsely scaled.

Petiole opaque, transverse, with a very small somewhat recurved lateral denticule. Postpetiole opaque, as broad as petiole, with a broad, apically truncate, posteriorly subdentate-projection on each side, curving slightly forward. Both peduncular segments finely reticulate-punctate with sparse, glistening appressed hairs.

Gaster opaque, elliptical, emarginate anteriorly mesad. First gastral tergite with a very narrow, not distinctly set off nor crested antero-lateral border. Tergites and sternites finely and rather sharply reticulate-punctate. Scales of gaster sparser, more slender than on head and thorax, not lying in distinctly excavated foveolae. Erect pile confine dto mandibles and to the 2–4th tergites and the sternites of the gaster."

Measurements (in mm) and indices: TL 3.84–5.52; HL 0.98–1.32; HW 1.24–1.76; EL 0.30–0.36; PW 0.92–1.38; PeW 0.37–0.57; PpW 0.44–0.66; HBaL 0.46–0.58; HBaW 0.10–0.15; CI 121.6–133.3; PI 127.5–134.8; PPeI 200.0–259.4; PPpI 204.2–209.1; HBaI 20.4–25.9.

S o l d i e r (Fig. 365) (description of Kempf, 1951). - "Length 7.5 mm. Median head length 1.95 mm; Weber's length of thorax 2.12 mm. Black; the following ferruginous: the four apical tarsal segments of the fore legs and the two apical segments of the mid and hind legs. Tips of last funicular segments orange-brown.

Head subopaque, somewhat shorter than wide. Frontal carinae strongly converging anteriorly, prolonged behind above the eyes in the form of a raised carinule, fading out before reaching the occipital corner. Upper surface of head distinctly convex, vertex with a pair of faint, not tuberculate median swellings on the posterior border. Occiput truncate, immarginate above; occipital angles form a scarcely projecting blunt, strong tubercle. Cheeks not marginate beneath in front; a vestigial margination beneath the eye is present. Eyes very little convex. Upper and lower surface of head finely and shallowly reticulate, the upper surface with rather dense, small foveolae in which a minute, not shiny, scale is visible. foveolae slightly more crowded, longer on occiput. Still larger and more deeply impressed on occiput and lower surface of head, containing a short decumbent, somewhat glistening seta.

Thorax subopaque. Anterior border arcuate, shoulder subangulate. Sides of pronotum diverging until reaching the lateral end of the transverse crest, having before the crest a stout, apically rounded tooth, projecting obliquely forwars and laterad. Transverse pronotal crest broadly interrupted mesad, and obsolescent towards the sides. Lateral border of pronotum angulate at the crest, and converging posteriorly behind the crest. Promesonotum, in profile, greatly convex. Promesonotal suture more or less distinct laterad, vestigial mesad. Sides of mesonotum subparallel with a small posterior, acute, lateral tooth. Mesoepinotal suture impressed and distinct. Basal face of epinotum transversely convex, with a small, blunt tooth antero-laterad, and a much longer and stronger, blunt spine on the posterior corner, slightly more divergent than in worker. Entire thorax finely and sharply reticulate-punctate. Dorsum of thorax and laterotergite of pronotum covered with rather dense, elongate deeply impressed setiferous foveolae. declivous face and posterior portion of the sides of the thorax with more or less vestigial, irregular, fine rugosities.

Petiole opaque, transverse, its sides subparallel, with a minute denticule. Postpetiole opaque, slightly broader than petiole, with a tapering, plate-like lateral projection, the apex of which is rounded in front, subdentate behind, curving slightly forward. Both segments finely reticulate-punctate, covered with vestigial foveolae and rugosities.

Gaster subopaque, elliptical, finely reticulate-punctate, not foveolate, deeply emarginate in front mesad. First gastral tergite anterolaterally sharply marginate, not forming a lamellate border.

All foveolae bear a decumbent seta, which is slightly flattened and glistening on thorax and peduncle. Erect setae on the terminal tergites and on the sternites of the gaster. First gastral tergite covered with minute, decumbent setae laterad, almost scaleless discad."

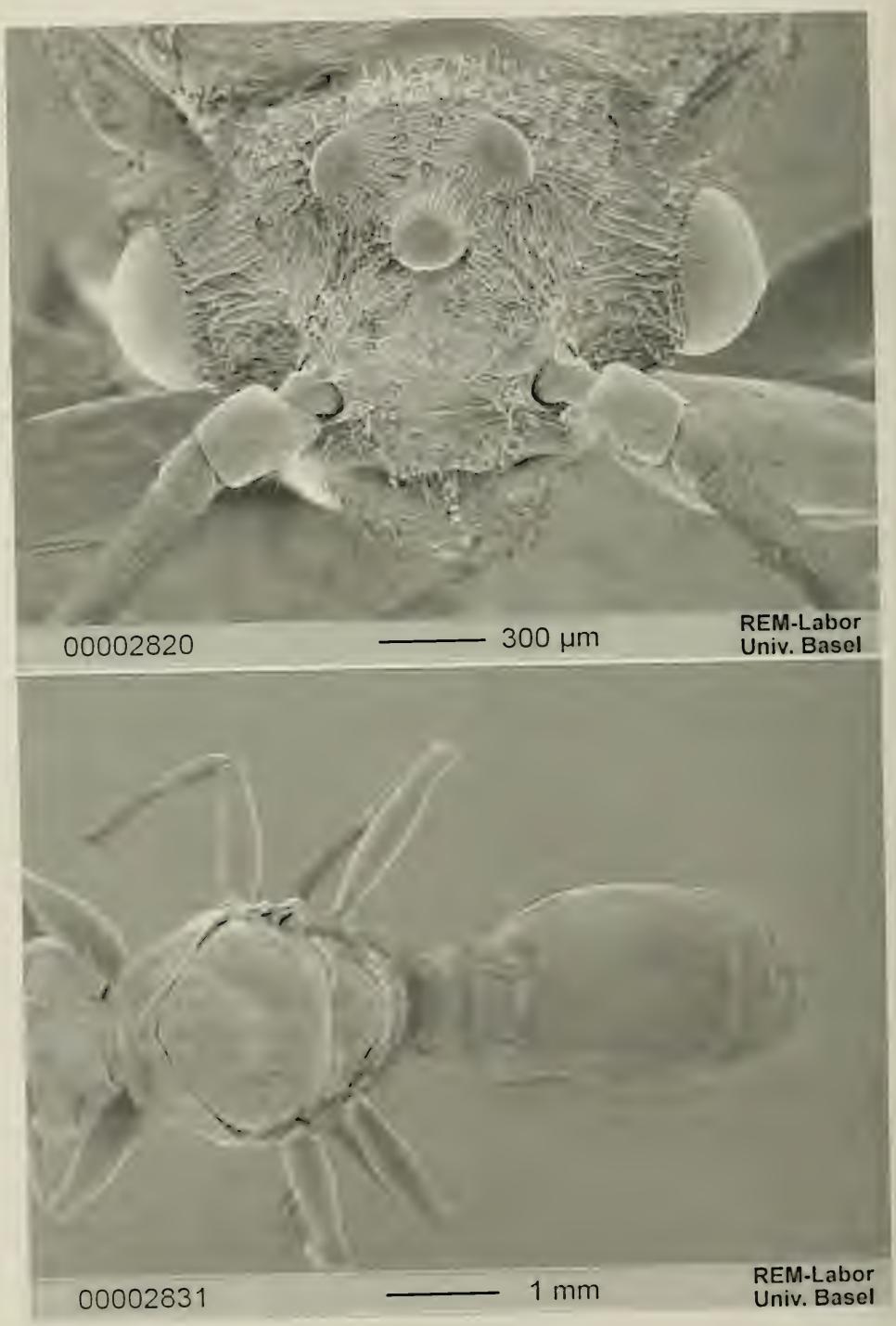


Fig. 68. *Cephalotes pusillus* (Klug). Male from Botucatu, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

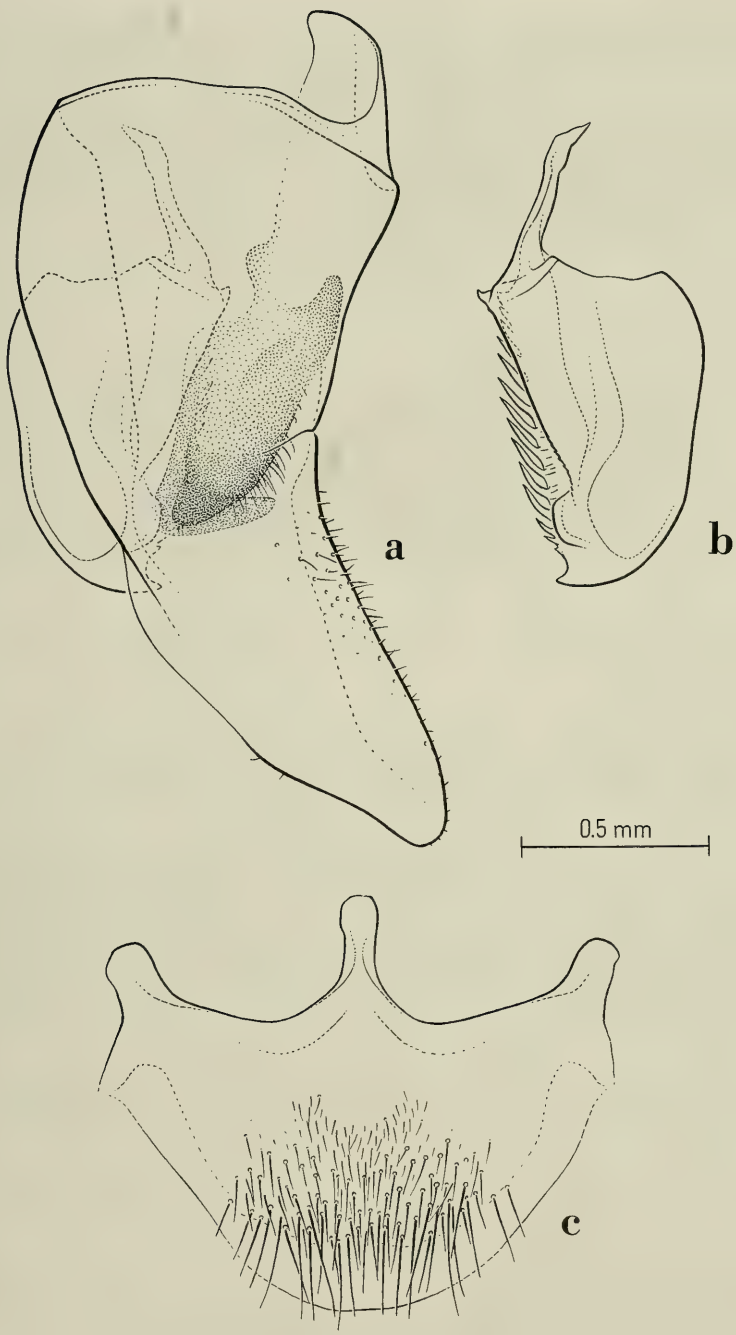


Fig. 69. *Cephalotes pusillus* (KLUG). Male from Botucatu, Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

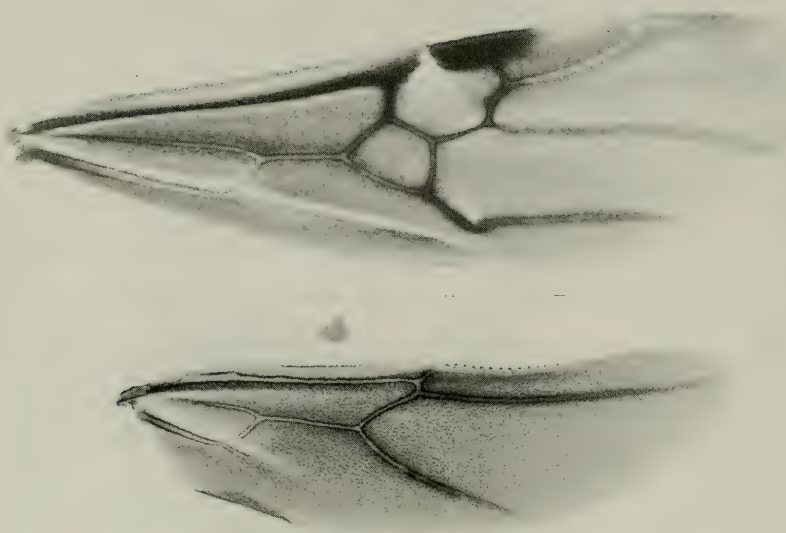


Fig. 70. *Cephalotes pusillus* (KLUG). Male from Botucatu, Brazil, fore and hind wings.

Measurements (in mm) and indices: TL 6.44–7.76; HL 1.60–1.90; HW 2.24–2.36; EL 0.45–0.48; PW 1.80–2.04; PeW 0.62–0.78; PpW 0.71–0.89; HBaL 0.64–0.66; HBaW 0.18–0.19; CI 124.2–130.0; PI 115.5–115.7; PPeI 261.5–290.3; PPpI 229.2–253.5; HBaI 28.1–28.8.

G y n e (Fig. 364) (description of KEMPF, 1951). - "Length 10.5 mm. Median head length 2.13 mm; interocular width 2.27 mm; Weber's length of thorax 3.17 mm. Black; tip of last funicular segment fuscous ferruginous. In general resembling *minutus*, from which it differs by the appreciably larger size, the black coloration of the appendages, the lack of the yellow maculae on the first gastral tergite. The head is shorter than wide, the upper face subopaque, greatly convex, with a distinct carinule laterad, below the eyes. Occiput subtruncate, immarginate above. Pronotum with a distinct transverse crest. Sides of petiole without a spine, or tooth; subparallel. Sides of thorax more extensively foveolate."

Measurements (in mm) and indices: TL 9.77–11.16; HL 1.76–1.96; HW 2.10–2.36; EL 0.45–049; PW 1.96–2.26; PeW 0.87–0.91; PpW 0.99–1.12; HBaL 0.72–0.75; HBaW 0.19; CI 119.3–127.3; PI 103.7–107.1; PPeI 222.7–248.3; PPpI 198.0–201.8; HBaI 25.3–26.4.

M a l e (Fig. 68). - Differing from *columbicus* in the following characters: head (eyes included) 1/3 broader than long; ocellar area strongly protruding. Scutellum much narrower posteriorly. Petiole more massive.

Genitalia and subgenital plate as in Fig. 69.

Wings as in Fig. 70.

Sculpture. Body with more impressed foveae, rugosities and punctures. Anterior third of the first gastral tergite with thin, superficial, longitudinal rugosities.

Colour. Black. Coxae, proximal third of femora, and tarsi brown. Distal thirds of the femora and tibiae yellowish.

Measurements (in mm) and indices: TL 9.00-9.44; HL 1.16–1.28; HW 1.44–1.60; EL 0.52–0.53; PW 1.48–1.60; PeW 0.92–0.93; PpW 1.04; HBaL 0.90–0.92; HBaW 0.14–0.15; CI 124.1–126.7; PI 95.0–100.0; PPeI 160.8–173.9; PPpI 142.3–153.8; HBaI 15.5–16.30.

Material examined. - **Colombia**: Meta: Carimagua, 370 m, 27.II.1972, 6 workers, M. L. CORN [MZSP]; Villavicencio, 1 worker, H. APOLIMAR [MZSP]. Amazonas: La Chorrera, 30 km downhill Río Igara Paraná, 26.II.1974, 1 worker, J. DESPLATS [MNHN].

Trinidad & Tobago: Trinidad: Aripo, Savannah, 29.IV.1913, 6 workers, R. THAXTER [MCZC]; same locality, 29.IV.1913, 1 worker [MCZC]; St. Augustine, 24.III.1935, 3 workers, N. A. WEBER [MCZC].

Venezuela: Delta Amacuro: Orinoco Delta, I-II.1935, 4 workers, N. A. WEBER [MCZC]. Distrito Federal: Caracas, III.1950, 4 workers, MARCUSEE [MZSP]. Anzoátegui: 18 km E Pariaguan, 236 m, 24.VI.1987, 1 worker, 1 soldier, M. A. IVIE [USNM]. Guarico: La Cruz-Ruviera, December 1925, 1 soldier, M. GRISOL [MNHN]. Cojedes: Chaparral, 10 km H. Piñero, near Baúl, 22.X.1986, 1 worker, E. M. CANCELLO & C. R. F. BRANDÃO [MZSP]. Bolívar: Moitaco, P. Anduze, 19.IX.1940, 4 workers, 3 soldiers [MCZC]; P. Anduze, Mar. 1942, 5 workers, 1 soldier [MCZC]; La Gran Sabana, 1370 m, 29.VI.1987, 1 worker, M. A. IVIE [USNM]; Kukenan River, 8 km SW of Mt. Roraima, 180 m, 3.I.1985, 3 workers, C. VOGT [MCZC]; Ciudad Bolívar, 23–30.I.1935, 8 workers, 1 soldier, N. A. WEBER [MCZC].

Guyana: Kartabo, Jul.-Aug.1920, 9 workers, 2 soldiers, W. M. WHEELER [MCZC, MZSP]; Bartica, 15-20.IX.1917, 1 worker, WM. BEEBE [MCZC]; Village nr. Courentyne, 5.VII.1936, 2 workers, 6 soldiers, N. A. WEBER [MCZC].

Brazil: no further locality, 5 workers, 2 soldiers, BATES [ZSMC]; Roraima: Rio Uraricuera, Ilha Maracá, III.1976, 1 worker, R. NEGRETT [MZSP]; 2 km from Ilha Maracá, 5 workers, 2 soldiers, C. R. F. BRANDÃO & E. M. CANCELLO [MZSP]. Amapá: Pacoval, 14.XII.1982, 2 workers, M. F. TORRES [MPEG]; Santana, Rio Amazonas, 14 & 17.VI.1966, 9 workers, W. WEYRAUCH [MZSP]. Amazonas: no further locality, 3 workers, H. W. BATES [ZSMC]; Paredão Rd., S of Manaus, 02 IX.1972, 3 workers, 3 soldiers, W. L. BROWN [MCZC]; Manaus, VII.1927, 1 gyne, ZIKÁN [MZSP]; same locality, 30.VIII & 3.IX.1962, 54 workers, 29 soldiers, K. LENKO [MZSP]; same locality, 3 soldiers, MANN & BAKER [MCZC]; same locality, Ponte Negra, 05.III.1971, 4 workers, 2 soldiers [MZSP]; same locality, km 10, Sítio das Jacas, 05.III.1983, 1 worker, 2 soldiers, A. Y. HARADA [INPA]; same locality, km 10, 10.IX.1983, 1 soldier, A. Y. HARADA [INPA]; same locality, BR 176, 19.II.1991. worker, 1 soldier, A. Y. HARADA [INPA]; Rio Tarumã, High Falls, 30.VIII.1962, 8 workers, 6 soldiers, W. L. BROWN [MCZC, INPA]; Praia, Rio Purus nr. Camutama, VIII.1971, 1 worker, J. BORRELLAS [MZSP]; Between Purus and Madeira rivers, VIII.1971, 3 workers, 3 soldiers, J. BORRELLAS [MZSP]. Pará: Castanhal, 2 workers, 1 soldier, GÖLDI [MHNG]; Óbidos, I.1905, 28 workers, A. DUCKE [MHNG]; Ponta de Pedras, 21.X.1982, 1 worker, W. L. OVERAL [MPEG]; Utinga, 6.I.1979, 3 workers, W. FRANÇA [MPEG]; Itaituba, Parque Nacional da Amazônia, 11–17.XI.1978, 1 worker, W. L. OVERAL [MPEG]; Serra Norte, N. 1 Campo, 15.V.1984, 2 workers [MPEG]; Gerotire, 3.V.1983, 1 soldier, W. L. Overal [MPEG]; Benevides, 14–17.IV1987, 7 workers, G. VENTURIERI [MPEG]; Carajás, 17.IV.1983, 1 worker, 1 soldier, MASCARENHAS et al. [MPEG]; Tocantins, Itaguatins, 17–19.VII.1989, 2 workers, F. F. RAMOS [MPEG]; Ilha Mexiana, 1906, 12 workers, 2 soldiers, HAGMANN [MHNG]; 4 km W of Vigia, 17.VIII.1962, 5 workers, 4 soldiers, W. L. BROWN [MCZC]; Santarém, VIII.1920, 3 workers, E. GARBE [MZSP]; Santarém, Taperinha, 2°54' S, 54°20' W, 22.VII.1975, 30.IX.1980, 4 workers, 1 soldier, R. J. JEANNE [MZSP]; same locality, 11–20.VII.1927, 1 worker, B. FINZI [MCZC]; Utinga nr. Belém, 14.VIII.1962, 12 workers, K. LENKO [MCZC]; Belém, II.1957, 1 gyne, P. F. PEREIRA [MZSP]; same locality, 12–19.VIII.1962, 41 workers, 5 soldiers, K. LENKO [MZSP]; Carajás, 21.VII.1985, 5 workers, C. R. F. BRANDÃO [MZSP]; Jacareacanga, X.1959, 1 gyne, M. ALVARENGA [MZSP]; Rio Purus, XI.1928, 1 worker, SAMPAIO [MZSP]; Conceição do Araguaia, 14.XI.1926, 2 workers, E. G. HOLT [USNM]; same locality, 28.XI.1978, 3 soldiers, R. B. NETO [MPEG]; 20 km S of Conceição do Araguaia 20.I.1983, 1 worker [MZSP]; Campo das Colinas, 30.XI.1928, 2 workers, 1 soldier, SAMPAIO [MZSP]; Boca do Cuminá-Miri, 19–26.I.1968, 13 workers, 1 soldier [MZSP]; Alter do Chão, Tapajós R., 21–23.II.1968, 14 workers, 4 soldiers, Exp. Dep. Zool. [MZSP]. Maranhão: Imperatriz, IV.1979, 30 workers, 10 soldiers, BARTOSZECK [MPEG]; Lago Rodriguez, 25–26.V.1979 & 12.VIII.1980, 16 workers, different collectors [MPEG]; Bacabal, 2.XI.1968, 6 workers, 3 soldiers, W. W. KEMPF [MZSP]; São Luís, 15.I.1959, 2 workers, D. WEIL [MZSP];

São Mateus, 16.VIII.1980, 1 worker, W. FRANÇA [MPEG]; Barra do Corde, 17.VI.1966, 2 workers, 2 soldiers [MZSP]; Estreito, 01.VI.1966, 10 workers, 2 soldiers [MZSP]; Igarapé Gurupi-Una, Aldeia Araçu, 50 km E de Canindé, 10.II.1966, 2 soldiers, 1 gyne, MALKIN [MZSP]. P i a u í : Antonio Almeida, 2 workers [MPEG]; Rio Uruçui-Preto, 20.II.1972, 4 workers, 2 soldiers, R. NEGRETT [MZSP]; 5 km E Oeiras, Fazenda Talhada, 13–17.XI.1991, 29 workers, 16 soldiers, C. R. F. BRANDÃO & P. MOUTINHO, [MZSP]; 20 km S of Floriano, Buriti Sol, 05–12.XI.1991, 71 workers, 7 soldiers, C. R. F. BRANDÃO & P. MOUTINHO [MZSP]; Canto do Buriti, 18–22.XI.1991, 1 soldier, S. T. AMARANTE & F. MARTINS [MZSP]; same locality and date, 10 workers, 4 soldiers, 1 gyne, C. R. FERREIRA BRANDÃO [MZSP]; Ribeiro Gonçalves, Est. Ecol. Uruçui-Una, 07 & 12.XII.1980, 10.XI.1982, 23 workers, A. J. ALMEIDA [MZSP]; Teresina, 4 workers [MPEG]; same locality, Sta. Teresa, 15.XI.1980, 2 soldiers, A. J. ALMEIDA [MZSP]. C e a r á : no further locality, 2 workers, MANN & BAKER [MCZC, USNM]; no further locality, 2 workers, 1 soldier, MANN [USNM]; Chapada do Araripe, 06.IV.1962, 8 workers, 12 soldiers, D. JAYCIS [MZSP]; same locality, 09.XI.1975, 3 workers, R. L. ARAÚJO [MZSP]; Barbalha, V.1969, 6 workers, M. ALVARENGA [MZSP]. R i o G r a n d e d o N o r t e : Natal, 14.III.1952, 2 workers, ALVARENGA [MZSP]; same locality, 1 worker, W. M. MANN [MCZC]; Mossoró, 15.XI.1975, 15 workes, R. L. ARAÚJO [MZSP]; Ceará-Mirim, 6 workers, W. M. MANN [MCZC]; Eduardo Gomes, 07.I.1989, 2 workers, A. Y. HARADA [INPA]. P a r a í b a : Mamanguape, VII.1957, 4 workers, Exp. Dep. Zool. [MZSP]; Corema, 1 worker, Exp. Dep. Zool. [MZSP]. P e r n a m b u c o : Recife, 1 soldier, BORGMEIER [MZSP]; Tapera, 9 workers, 5 soldiers, 2 gynes, 1 male, PICKEL [MZSP]; Caruaru, 1 worker, PICKEL [MZSP]; same locality, IV.1972, 4 workers, M. ALVARENGA [MZSP]; Serra Negra, 23.XI.1987, 20 workers, 4 soldiers, 1 gyne, M. C. LEAL [MZSP]; Floresta, Fazenda Campo Bons, 20–27.VI.1971, 3 workers, Exp. ABC-MZUSP [MZSP]; Serra dos Prazeres nr. Recife, 09.VII.1944, 12 workers, R. L. WENZEL [MZSP]. A l a g o a s : Maceió, 13.XII.1967, 5 workers, 1 soldier, M. C. ARCANJO [MZSP]; Coruripe, 2.X.1979, 10 workers, F. M. OLIVEIRA [MPEG]. R o n d ô n i a : Porto Velho, 1 worker, ALVARENGA [MZSP]; Porto Velho, Rio Tapirapé, IV.1964, 1 gyne, R. T. LIMA [MZSP]; Vilhena, VIII.1971, 9 soldiers, J. BORRELLAS [MZSP]; same locality, 26.VII.1983, 2 workers, A. Y. HARADA [INPA]; same locality, BR. 364, Terreno do João, 02.VIII.1983, 7 workers, A. Y. HARADA [INPA]; same locality, 02.VIII.1983, 1 worker, A. Y. HARADA [INPA]; same locality, Est. Colorado, 29.VII, 3.VIII.1983, 2 workers, A. Y. HARADA [INPA]; Ouro Preto do Oeste, 8.IV.1985, 1 worker, 2 soldiers, J. DIAS [MPEG]; Ji-Paraná-Gleba, 19.II.1983, 1 worker, J. R. ARIAS [INPA]. A c r e : Rio Branco, 25.X–8.XI.1991, 1 worker, F. RAMOS et al. [MPEG]; Rio Branco, 16.V.1952, 2 workers, ALVARENGA [MZSP]; Rio Branco, Uranduique, VI.1960, 1 worker, MACHADO & PEREIRA [MZSP]; Rio Branco, Suzumu, X.1955, 1 worker, ALVARENGA & MARTINEZ [MZSP]. G o i á s : Jataí, XI.1971, 3 workers, 1 soldier, F. M. OLIVEIRA [MZSP]; Jataí, Fazenda Cachoeirinha, 26.X.1962, 52 workers, 7 soldiers, 3 gynes, Exp. Dep. Zool. [MZSP]; Jataí, Fazenda Aceiro, 30.X.1962, 10 workers, 6 soldiers, Exp. Dep. Zool. [MZSP]; Anápolis, km 46 on road to Goiania, 10–12.V.1971, 3 workers, 3 soldiers, W. L. & D. E. BROWN [MCZC]; Filadelfia, 15.II.1949, 1 worker, GONÇALVES [MZSP]; Goiatuba, 21.XI.1960, 1 gyne [MZSP]; Anápolis, 27.III.1956, 12.II.1958, 11.I.1966, 13 workers, 1 soldier, 1 gyne, W. W. KEMPF [MZSP]; Alto Paraíso, Fazenda Bona Espera, 01–0 7.VII.1991, 8 workers, C. R. F. BRANDÃO et al. [MZSP]; 7 km NW Alto Paraíso, Morro das Cobras, 01–07.VII.1991, 2 workers, C. R. F. BRANDÃO et al. [MZSP]; Alvorada do Norte, Fazenda Matos, 08–12.VII.1991, 16 workers, 1 soldier, C. R. F. BRANDÃO [MZSP]; same locality and date, 3 workers, 3 soldiers, S. T. P. AMARANTE & C. F. MARTINS [MZSP]; Campinas, IV.1927, 23.VII.1928, 2 workers, 2 soldiers, C. P. SCHWARZMAIER [MZSP]; Araguacema, 25–29.I.1983, 1 worker, J. A. RAFAEL [MZSP]. B a h i a : Encruzilhada, 960 & 980 m, XI.1972, XI.1973, XI.1974, 109 workers, 2 soldiers, 1 gyne, 3 males, SEABRA & ALVARENGA [MZSP]; Mucugê, 6–12.XII.1990, 3 workers, C. R. F. BRANDÃO et al. [MZSP]; Itaberaba, Fazenda Riacho do Uruçu, XII.1990, Caatinga, 2 workers, S. T. P. AMARANTE [MZSP]; same locality, 1–5.XII.1990, 36 workers, 3 soldiers, C. R. F. BRANDÃO et al. [MZSP]; Planalto Barroso, 01.II.1980, 3 workers, P. E. VANZOLINI [MZSP]; Sta. Rita de Cássia, 14–17.VII.1991, 7 workers, S. T. P. AMARANTE & C. F. MARTINS [MZSP]; same locality, Riacho Veredão, 13–18.VII.1991, 19 workers, 3 soldiers, C. R. F. BRANDÃO [MZSP]; Boca do Rio, Salvador, IX.1981, 3 workers, C. R. F. BRANDÃO [MZSP]; Maracás, Fazenda Maria Inácia, mata cipó,

24–29.XI.1990, 89 workers, 17 soldiers, C. R. F. BRANDÃO et al. [MZSP]; same locality, 25.XI.1990, 5 workers, S. T. P. AMARANTE [MZSP]; Ilhéus, Itabuna, X.1986, 3 workers, 2 soldiers, J. DELABIE [MZSP]; Maiquinique, 17.IX.1993, 2 workers, 1 soldier, 1 gyne, DELABIE & BRITO [CPCC]; Ilhéus, 26.II.1995, 1 male, J. H. C. DELABIE [CPCC]. Distrito Federal: Gama, nr. Brasilia, 10.II.1964, 5 workers, H. M. CANTES [MZSP]; Brasilia, VIII.1961, 1 worker, N. L. H. KRAUSS [USNM]; same locality, 7.V.1979, 5 workers, R. B. NETO [MPEG]; Res. Biol. Águas Emendadas, different dates, 129 workers, 50 soldiers, C. R. F. BRANDÃO et al. [MZSP]. Mato Grosso: no further locality, 2 workers, 1 soldier [MHNG]; no further locality, 1 gyne, GERMAIN [NHMB]; Sinop, 55°37' W, 12°31'S, X.1974, 1 worker, M. ALVARENGA [MZSP]; U. H. Manso, campo cerrado grotão, 13–16.VIII.1988, 59 workers, 7 soldiers, H. C. MORAIS [MZSP]; Barra dos Bugres, Reserva Ecológica Serra das Araras, 24.I.1986, 2 soldiers, M. ZANUTO [MPEG]; Chapada, I.1960, VII.1961, 4 workers, C. AMANN [MZSP]; same locality, V.1959, 1 worker, Fr. CANUTO [MZSP]; Chapada dos Guimarães, XI.1963, 2 workers, ALVARENGA [MZSP]; same locality, II.1985, 5 workers, C. R. F. BRANDÃO [MZSP]; Utiariti, Rio Papagaio, 07–0 8, 11, 23, 30–31.X, 02 & 12.XI.1966, 79 workers, 25 soldiers, 13 gynes, LENKO & PEREIRA [MZSP]; same locality, 325 m, VII & VIII.1961, 29 workers, 3 soldiers, K. LENKO [MZSP]; same locality, Fazenda Buriti, 14–21.XI.1982, 3 workers, M. ZANUTO [MPEG]; Diamantino, 21.X.1966, 18 workers, 2 soldiers, K. LENKO [MZSP]; Alto do Céu, 8 km N Fazenda Buriti, Chapada dos Guimarães, 10.II.1986, 1 worker, C. R. F. BRANDÃO & F. H. CAETANO [MZSP]; Chapada dos Guimarães, Fazenda Buriti, 9–14.II.1986, 2 workers C. R. F. BRANDÃO & F. H. CAETANO [MZSP]; Buriti, 21.VII.1972, 5 workers, 1 soldier, R. WILLIANS [MZSP]; Rondonópolis, 10.VI.1952, 3 workers, C. GILBERT [MZSP]; same locality, 14.VII.1972, 17 workers, 11 soldiers, R. N. WILLIANS [MZSP]; same locality, 06.III.1971, 8 workers, 3 soldiers, W. W. KEMPF [MZSP]; same locality, 11.XII.1950, 2 workers, 3 soldiers, 1 gyne, DIRINGS [MZSP]; same locality, 18.XII.1990, 1 worker, DIRINGS [MZSP]; same locality, Area Indigena Tadarimana, 05.X.1990, 24 & 31.X.1991, 13 workers, 1 soldier, M. T. TAVARES [MZSP]. Mato Grosso do Sul: Xavantina, Rio das Mortes, 21.VII.1976, 2 workers, 1 soldier, W. W. KEMPF [MZSP]; Itaum, III.1974, 1 worker, M. ALVARENGA [MZSP]; Rio Paraguay, Fazenda Acurizal, 18.VIII.1977, 8 workers, G. B. SCHALLER [MCZC]; Campo Grande, 07.VI.1952, 3 workers, GILBERT & MÜLLER [MZSP]; same locality, 09.X.1961, 12 workers, 1 soldier, F. M. OLIVEIRA [MZSP]; Três Lagoas, Fazenda Retiro das Telhas, 28.V, 13 & 23.VI.1964, 154 workers, 22 soldiers, 1 gyne, Exp. Dep. Zool. [MZSP]; Três Lagoas, Fazenda Floresta, 19.IX.1964. 3 worker, 2 soldiers, 1 gyne [MZSP]; Três Lagoas Fazenda Canaã, XI.1966, I.1967, VI.1967, 08–14.I.1970, 38 workers, 6 soldiers, 1 gyne, F. LANE [MZSP]; Três Lagoas, left side of Sucuriú river, Fazenda Canaã, 30.X.1966, 3 workers, 2 males, F. LANE [MZSP]; Estação Ecológica Taiamã (Pantanal), 20.XI.1980, 3 workers, G. GUARIU [INPA]; Palmito, Município Três Lagoas, 20.V.1964, 8 workers, Exp. Dep. Zool. [MZSP]; Córrego da Onça, Fazenda Yamaguti, Município Três Lagoas, VI.1964, 44 workers, 9 soldiers, Exp. Dep. Zool. [MZSP]; Barragem da Ilha Solteira, Três Lagoas, 29.XI.1964, 7 workers, 9 soldiers, Exp. Dep. Zool. [MZSP]; Três Lagoas, Fazenda Beija Flor, 22.VI.1964, 11 workers, 2 soldiers, Exp. Dep. Zool. [MZSP]; same locality, Fazenda Dr. José Mendes, 22 & 26.V, 16.VI, 14–24.X.1964, 42 workers, 21 soldiers, Exp. Dep. Zool [MZSP]; Cáceres, 02.XII.1955, 4 workers, M. ALVARENGA [MZSP]; Dourados, Colônia Vicentina, I.1962, 12 workers, 1 soldier, A. MUELLER [MZSP]; Corumbá, 6 workers, 1 soldier, SILVESTRI [MCZC, NHMB]; Corumbá, Serra do Urucum, 26–30.XI.1960, 80 workers, 12 soldiers, 1 gyne, 6 males, K. LENKO [MZSP]; Imbirussu, Corumbá, 1.XII.1960, 5 workers, 1 soldier, K. LENKO [MZSP]; Nioaque, 23 & 25.VII.1971, 2 workers, R. TRAVASSOS [MZSP]; Coxim, 09.III.1971, 3 workers, W. W. KEMPF [MZSP]; Ilha Taiamã, R. Paraguai, 07 & 10. VIII.1980, 12 workers, 9 soldiers, C. R. F. BRANDÃO [MZSP]; Limoeiro, 10 km S of Ilha Taiamã, 3.VIII.1980, 5 workers, C. R. F. BRANDÃO [MZSP]. Espírito Santo: Linhares, IX.1972, 3 workers, M. ALVARENGA [MZSP]; Pedro Canário, Con. da Barra, X.1972, 1 worker, 1 soldier, M. ALVARENGA [MZSP]. Minas Gerais: no further locality, 1905, 1 worker, Coll. E. GOUNELLE [MNHN]; no further locality, 2 workers, Thayer Exp. [MCZC]; no further locality, 10 workers, E. LUJA [NHMB]; Sertão de Diamantina, Fazenda das Melancias, 10.XI.1902, 2 males [NHMB]; Serra do Cipó, 16 km Cardeal Mota, 03–07.X.1981, 1 worker, A. F. G. SILVA [MZSP]; same locality, 8 workers, 1 soldier, R. V. S. PAIVA [MZSP]; Nova Lima, 26.IX.1992, 17 workers, 11 soldiers, A. C. F. LARA [MZSP];

Viçosa, 18.VII.1989, 17 workers, 2 soldiers, J. M. DINIZ [MZSP]; Pirapora, 26 workers, 1 soldier, 4 males, E. GARBE [NHMB]; Barbacena, 31.VIII.1975, 19 workers, 18 soldiers, R. L. ARAUJO [MZSP]; Serra da Caraça (Engenho), 800 m, XI.1961, 1 worker, 1 gyne, KLOSS et al. [MZSP]; same locality, Sta. Barbara, 23–25.XI.1960, 1 soldier, ARAUJO & MARTINS [MZSP]; same locality, 1380 m, XI.1961, 75 workers, 20 soldiers [MZSP]; Governador Valadares, 12 & 18.I.1958, 17 workers, 2 soldiers, K. LENKO [MZSP]; Carmo da Cachoeira, VIII.1957, 1 worker, J. V. BRETAS [MZSP]; same locality, XI.1957, 1 worker, E. V. BRETAS [MZSP]; Jacutinga, 10.X.1928, 1 worker, 1 soldier, O. CONDE [MZSP]; Sete Lagoas, XI.1963, 5 workers, G. R. KLOSS [MZSP]; same locality, III.1963, 5 workers, WERNER et al. [MZSP]; Varginha, I.1960, 3 workers, 1 soldier, 1 gyne, ALVARENGA & SEABRA [MZSP]; Arassuaí, IX.1926, 3 workers, 2 soldiers, P. THIEMEN [MZSP]; Pedra Azul, XI.1970, I.1971, 7 workers, F. M. OLIVEIRA [MZSP]; same locality, 800 m, XI.1972, 5 workers, 1 gyne, SEABRA & ALVARENGA [MZSP]; same locality, mata de galeria, 21.XI.1990, 11 workers, 1 soldier, C. R. F. BRANDÃO et al. [MZSP]; Morro da Garça, 18–20.X.1964, 1 worker, 1 soldier, Exp. Dep. Zool. [MZSP]; Mons. Paulo, 05.XII.1956, 6 workers, 2 soldiers, 1 gyne, V. SANTOS [MZSP]; Belo Horizonte, 1–6.XI.1919, 3 workers, Cornell University Expedition [MZSP]; Cachoeira do Marimbondo, 4.III.1965, 1 worker, VIZOTTO [MZSP]; Serro, VI.1976, 1 worker, R. NEGRETT [MZSP]; Unaí, III.1976, 1 worker, A. NEGRETT [MZSP]; Itaquaquecetuba, 1 worker, 2 soldiers, 1943, H. L. PARKER [MCZC]; Ladário, 23.VI.1952, 5 workers, GILBERT & MÜLLER [MZSP]; Tiradentes, I.1957, 3 workers, R. MUELLER [MZSP]; same locality, 30.VII.1975, 9 workers, 1 soldier, R. L. ARAÚJO [MZSP]; Itaobim, 26.VI.1966, 6 workers, H. REICHARDT [MZSP]; Tapuirama, Município Uberaba, 23.X.1962, 41 workers, 11 soldiers, K. LENKO [MZSP]. S ã o P a u l o : no further locality, 1909, 2 soldiers, JHERING [MHNG]; São Paulo, Villa Frontim, 7.XII.1905, 2 workers, H. VON JHERING [USNM]; Cachoeira Paulista, 25.VIII.1961, 3 workers, 3 soldiers, 1 gyne, F. GROSSMANN [MZSP]; Castilho, left side of Paraná river, 18.X.1964, 3 workers, Exp. Dep. Zool. [MZSP]; Avaré, Fazenda Guarujá, 22.IV.1972, 1 worker, F. LANE [MZSP]; Nova Europa, Fazenda Itaquerê, 24–25.VIII, 28–29.XI, 01.XII.1963, 16, 19–20.VII.1964, 99 workers, 29 soldiers, K. LENKO [MZSP]; Avaré, 15.XI.1971, 17 workers, F. LANE [MZSP]; Ubatuba, 15.VIII.1967, 12 workers, 1 soldier, P. C. MONTOUCHET [MZSP]; Cajuru, 21°17' S, 47°18' W, different months in 1992 & 1993, 313 workers, 64 soldiers, A. SILVESTRI [MZSP]; Caraguatatuba, Res. Florestal, 40 m, 2.IV, 22.V, 1.VI.1962, 12.VII.1965, 40 workers, 8 soldiers, Exp. Dep. Zool. [MZSP]; Ibitinga, Fazenda Itaquerê, 21.VI.1965, 12 workers, 4 soldiers, K. LENKO [MZSP]; Boa Esperança do Sul, Fazenda Itaquerê, 25.VII, 28.XI.1963, 25 & 27.I, 17–20.VII.1964, 119 workers, 27 soldiers, K. LENKO [MZSP]; Jundiaí, Reserva Japi, 04.VI.1973, 1 worker, 2 soldiers, J. M. DINIZ [MZSP]; Embu, 06.II.1971, 22–30.I.1972, 7 workers, 2 soldiers, 1 male, L. LANE [MZSP]; Cachoeira das Emas, Município Piraçununga, Feb.1967, 3 workers, 5 soldiers, W. L. BROWN [MCZC]; São Sebastião, 05.II.1953, 7 workers, 2 soldiers, W. W. KEMPF [MZSP]; same locality, 30.I.1955, 3 workers, B. FLEDDERMANN [MZSP]; Ilha Bela, Ilha de São Sebastião, 29.XI.1964, 4 workers, 3 soldiers, 1 gyne, 4 males, H. URBAN [MZSP]; Avaré, Fazenda Guarujá, 22.IV.1972, 5 workers, 1 soldier, L. LANE [MZSP]; São Roque, 25.XII.1971, 4 workers, 2 soldiers, L. LANE [MZSP]; Mirassolâ, Fazenda B. Grande, 07.V.1972, 3 soldiers, J. M. DINIZ [MZSP]; São Paulo, Ipiranga, 12.XI.1906, 3 workers, 2 soldiers, 1 gyne, H. LUEDERWALDT [MZSP]; Franca, I.1911, 6 workers, E. GARBE [MZSP]; São Paulo, V.1954, IV.1961, 2 workers, N. L. H. KRAUSS [USNM]; Mogi Guaçu, 19.V.1958, 11 workers, K. LENKO [MZSP]; same locality, Fazenda Campininha, 20–22.V. & 09.VIII.1977, 7 workers, 2 soldiers, 1 gyne, H. C. MORAIS [MZSP]; same locality, 19.V.1958, 3 workers, 1 soldier, K. LENKO [MZSP]; São Bernardo, 18.XI.1961, 9 workers, 7 soldiers, 8 gynes, 6 males, WERNER [MZSP]; São Bernardo do Campo (Vila Paulicéia), 24.XII.1960, 1 worker, WERNER [MZSP]; Monteiro Lobato, 1.X.1961, 4 workers, 4 soldiers, L. TRAVASSOS [MZSP]; Itú, Fazenda Pau d' alho, 27.XII.1959, 14.VIII & 09.X.1960, 15 workers, 2 soldiers, WERNER & MARTINS [MZSP]; same locality, 17.IX.1960, 14 workers, 1 soldier, B. PÉRSIO [MZSP]; same locality, 04.XII.1988, 1 worker, AMARANTE [MZSP]; Itú, 02.II.1959, 3 workers, F. LANE [MZSP]; Barueri, 22.XII.1957, 36 workers, 5 soldiers, [MZSP]; same locality,18.X.1958, 37 workers, 24 soldiers, K. LENKO [MZSP]; Parelheiros, 20.XII.1975, 2 workers, L. R. FONTES [MZSP]; Araçatuba, X.1961, 1 worker, J. LANE & RABELLO [MZSP]; Ribeirão Preto, Fazenda Dumont, 09.VII & 08.VIII.1927, 1 worker, 1 soldier, 1 gyne, 1 male, O. CONDE [MZSP]; Magda, Rio Preto, 7 workers, 1 soldier, J. LANE [MZSP]; Salto Grande,

II.1911, 2 workers, H. LUEDERWALDT [MZSP]; Agudos, V.1958, 11 workers, 1 soldier, R. MUELLER [MZSP]; same locality, 26.X.1952, 12.IX.1953, 7 workers, 2 soldiers, G. GILBERT [MZSP]; same locality, 03–19.III, 25 & 28.V.1952, 11 workers, 6 soldiers, W. W. KEMPF [MCZC, MZSP]; Rio Claro, Horto Florestal, 27.IV.1970, 3 workers, V. GAMA [MZSP]; same locality, 18.I.1962, 9 workers, 3 soldiers, REICHARDT [MZSP]; Anhembi, Fazenda B. Rico, 06–08.IX.1959, 6 workers, L. T. F. & A. BARROSO [MZSP]; same locality, 14.II.1969, 5 workers, 1 soldier, W. W. KEMPF et al. [MZSP]; Teodoro Sampaio, Município Mirante, III.1958, 3 workers, 3 soldiers, FORETTINI [MZSP]; same locality, VIII.1973, 1 worker [MZSP]; Pico de Jaraguá, 27.VI.1962, 4 workers, 2 soldiers, E. AMANTE [MZSP]; Guaratinguetá, 15.XI.1958, 2 workers, 1 soldier, W. W. KEMPF [MZSP]; Pirapora, VI.1922, 2 workers, E. GARBE [MZSP]; Venceslau Braz, V.1958, 2 workers, 1 soldier, I. YAMASHITA [MZSP]; Itararé, 2 workers, O. FILHO [MZSP]; Amparo, 28.II.1964, 9 workers, W. W. KEMPF [MZSP]; Pindamonhangaba, 1 gyne, SCHWARZMEIER [MZSP]; Caraguatatuba, Praia Palmeiras, 31.V.1962, 1 worker, Exp. Dep. Zool. [MZSP]; same locality, Praia Massaguaçú, 28–30.V.1962, 7 workers, 1 soldier, Exp. Dep. Zool. [MZSP]; Juquiá, Fazenda Sta. Rita, 30.I.1988, 1 worker, V. C. SILVA [MZSP]; São José do Rio Preto, 25.II.1965, 17 workers, 3 soldiers, L. D. VIZOTTO [MZSP]; Serra Negra, Colônia da Força Pública, 13.VIII.1965, 21 workers, 2 soldiers, P. BIASI [MZSP]; Paranapanema, km 241, 18.X.1967, 1 worker, W. W. KEMPF [MZSP]; Campinas, 1 worker, 2 soldiers, A. FERREIRA [MZSP]; same locality, 2 workers, 1 soldier, 1 gyne, 2 males, O. FILHO [MZSP]; same locality, 19.III.1939, 1 worker, P. A. BERRY [USNM]; Pedreiras, 4 workers, 1 soldier, 08.IV.1926, SCHWEBEL [MZSP]; Campo Limpo, 20.II.1966, 3 workers, 3 soldiers, W. W. KEMPF [MZSP]; Monte Mor, 23.XII.1965, 4 workers, A. FERRI [MZSP]; Jaguarí, XI.1965, 1 worker, 1 gyne, G. R. KLOSS [MZSP]; Jundiaí, 14.X.1961, 6 workers, 23 soldiers, 6 gynes, WERNER [MZSP]; Itanhaem, V.1928, 3 workers, SPITZ [MZSP]; Itirapina, 18.III.1966, 1 worker, W. KEMPF [MZSP]; same locality, II.1990, 1 worker, C. DANSA & R. ROCHA [MZSP]; Nazaré Paulista, 28.VII.1991, 3 workers, 1 soldier, B. H. DIETZ [MZSP]; Lindóia, IV.1926, 3 workers, C. WIRTH [MZSP]; Piraçununga, Cerrado das Emas, 05.IX.1966, 1 soldier, A. A. ROCHA [MZSP]; Itu, XI.1957, 2 workers, 1 soldier, P. F. PEREIRA [MZSP]. Rio de Janeiro: no further locality, 1 worker [NHMB]; no further locality, 13 workers, 2 soldiers [ZSMC]; no further locality, in Uva stalks, intercepted in an U.S. Port of Entry, 12.VI.1985, 1 worker, 1 soldier, C. THOMAS [USNM]; Cascadura, 07.XII.1906, 11 workers, WACHET [MZSP]; same locality, 4 workers, 2 soldiers, JHERING [MHNG]; Alto da Boa Vista, Montanha dos Orgãos, 1902, 1 worker (syntype of var. *brevispinosa*), E. R. WAGNER [NHMB]; Rio Manso, IV.1919, 2 workers, 1 soldier, T. BORGMEIER [MZSP]; Jacarepagua, 22.II.1920, 1 worker, E. G. HOLT [USNM]; Sapopemba, 5 workers, 4 soldiers, WACKET [MZSP]; same locality, 10 workers, 3 soldiers, JHERING [MHNG]; Marambaia, 3 workers, I.1960, R. MUELLER [MZSP]; Conceição de Macabu, IX.1978, 8 workers, 1 soldier, M. ALVARENGA [MPEG]; Campo Belo, 1906, 4 workers, 1 soldier, H. LUEDERWALDT [MZSP]; Petrópolis, 1918, 3 workers, T. BORGMEIER [MZSP]; same locality, I.1956, 1 worker [MZSP]; Deodoro, V.1936, 6 soldiers, A. RONNA [MZSP]; Represa do Rio Grande, IV.1962, 7 workers, 2 soldiers, F. M. OLIVEIRA [MZSP]; same locality, VII.1972, 5 workers, M. ALVARENGA [MZSP]; Silva Jardim, Mar. & Aug. 1974, 4 workers, F. M. OLIVEIRA [MZSP]; Porto das Caixas, VI.1928, 1 gyne, O. CONDE [MZSP]; Rio Bonito, 20.VII.1974, 1 worker, J. A. WINDER [MZSP]; Barrão de Inhomirim, Raiz da Serra, 07.XI.1921, 1 soldier, T. BORGMEIER [MZSP]; Raiz da Serra, 6 workers, T. BORGMEIER [MCZC]; Guaratiba, X.1929, 4 workers, T. BORGMEIER [MZSP]; Itatiaia, II.1974, 1 worker, F. LANE [MZSP]; same locality, 4 workers, 3 soldiers, 2 gynes, J. F. ZIKÁN [MZSP]; Quissamã, 14.I.1922, 3 soldiers, T. BORGMEIER [MZSP]. PARANÁ: Rolândia, 01–15.XI.1951, 13 workers, 2 soldiers, W. W. KEMPF [MZSP]; Rio Paraguai, 6 workers, 2 gynes, K. FIEBRIG [MCZC]. Santa Catarina: S. Manoel, 13.IV.1964, 1 soldier, F. LANE [MZSP]; Nova Teutônia, XII.1974, 300–500 m, 3 workers, F. PLAUMANN [MZSP]. Rio Grande do Sul: no further locality, 1 worker [MHNG]; S. Augusto, XII.1975, 1 worker, B. ROPPA [MZSP].

Peru: Chanchamayo, 800–900 m, 1939, 01.I.1959, 5 workers, 1 soldier, WEYRAUCH [MZSP]. Loreto: Sta. Ana, Río Urubamba, 1100 m, 01.XII.1940, 1 worker, 1 gyne, WEYRAUCH [MZSP]. Cajamarca: Jaen, 700 m, VII.1947, 3 workers, WEYRAUCH [MZSP]; Nanchoc Quebrada, 6°57' S, 79°15' W, 400 m, 21.XII.1984–17.I.1985, 1 worker, J. M. CARPENTER [MCZC]. Junín: El Campamiento, Col. Perene, 20.VI.1920, 2 workers,

Cornell Univ. Exp. [MZSP]; Río Perené, 1911, 2 workers, 2 soldiers, TOWSEND [MCZC]. C u z c o : La Convencíon, 30.VIII.1973, 2 workers, J. A. ESCALANTE [MZSP]; C. Corado, Quillabamba, 1300–1600 m, 18.V.1964, 2 workers, B. MALKIN [MZSP].

Bolivia: between Bayova and Guagua, 6 workers, 1 soldier, LIZER & DELÉTANG [NHMB]; Chipiri, boring stems of Avocados trees, 2 workers, 5 gynes, F. O. TERAN [USNM]; Canamina, Jul. 1921–22, 1 worker, 1 soldier, W. M. MANN [USNM]; Espia, Río Bopi, 1 worker, 3 soldiers, W. M. MANN [MZSP, USNM]. B e n i : Trinidad, 3 workers, N. KUSNEZOV [MZSP]; Rosario, Lago Rogagua, 6 soldiers, 1 male, W. M MANN [MZSP]; Rurrenabaque, Oct.1921–22, 1 soldier, 1 male, W. M. MANN [USNM]; Huachi, Sept. & Dec. 1921–1922, 5 workers, 1 soldier, W. M. MANN [MZSP, USNM]; Reyes, 1921–22, 1 worker, W. M. MANN [USNM]; El Beni, NE San Borja, 28.VII.1988, 1 worker, R. W. BROOKS [USNM]. L a P a z : Ixiamas, Dec. 1921–22, 2 workers, 4 soldiers, W. M. MANN [MZSP]. S a n t a C r u z : Sara, Nueva Moka, 1 gyne, A. MARTINEZ [MZSP].

Argentina: S a l t a : Orán, Abra Grande, 18.IV–05.V.1969, 2 workers, C. PORTER [MCZC]; Río de la Trentesa, XII.1957, 1 soldier, J. DAGUERRE [USNM]; Río Pescado, 70 km N Orón, 360 m, 27.II.1964, 2 workers, GOEYRAUCH [MZSP]; Aquaray, XII.1959, 1 worker, A. MARTINEZ [MZSP]; Aguas Blancas, 2 workers, N. KUSNEZOV [MZSP]; Yuto, 2 workers, soldier, N. KUSNEZOV [MZSP]. F o r m o s a : Puerto Pilcomayo, 34 workers, 10 soldiers, N. KUSNEZOV [MHNG, MZSP]; Las Lomitas, 3 workers, 1 soldier, N. KUSNEZOV [MZSP, USNM]. C h a c o : no further locality, 1 worker (type of ab. *rufescens*), v. STEIGER [NHMB]. S a n t i a g o d e l E s t e r o : Girardet, 5 workers, A. MERKLE [NHMB]. C o r r i e n t e s : San Roque, 3 workers, J. BOSQ. [NHMB]. M i s i o n e s : no further locality, 2 workers, C. BRUCH [NHMB]; Loreto, 14 workers, 1 gyne, 6 males, N. KUSNEZOV [MHNG]; Manuel Belgrano, 2 soldiers, N. KUSNEZOV [MZSP]; Iguazú, X.1964, 2 workers, A. MARTINEZ [MZSP]; Ignacio, V.1961, 1 worker, N. L. H. KRAUSS [USNM]; San Ignacio, Villa Lutécia, 1910, 1 worker (syntype of var. *brevispinosa*), E. R. WAGNER [NHMB]; Cerro Cora, 1 soldier (syntype of var. *brevispinosa*), v. STEIGER [NHMB]. S a n t a F é : S. Felicia, 1 worker, 2 soldiers [MZSP]. C ó r d o b a : Cruz Grande, 1 soldier (syntype of var. *brevispinosa*), v. STEIGER [NHMB].

Paraguay: no further locality, 1 soldier (syntype of var. *brevispinosa*), K. FIEBRIG [NHMB]. C h a c o : no further locality, 5 workers, B. FINZI [MCZC]. C o n c e p c i ó n : Puerto Max, 19.X.1979, 3 workers, J. L. PERRET [MHNG]. P r e s i d e n t e H a y e s : Laguna Pora, 60 km NE Filadelfia, 12.X.1978, 1 soldier, 1 gyne, 2 males, K. H. REDFORD [MCZC]. A l t o P a r a n á : Pastoreo, 30.IX, 23–25.X, 02.XII.1974, 11 workers, P. DUELLI [MZSP]; same locality, 21.I., 1 worker, D. WEES [MCZC]. C e n t r a l : Luque, 13.VII.1961, 2 workers, N. L. H. KRAUSS [USNM]. L a C o r d i l l e r a : Asunción, Villa Mora, 5 workers, SPEGAZZINI [NHMB]; Bernardino, 11 workers, 9 soldiers, 4 gynes, K. FIEBRIG [MHNG, USNM, ZSMC].

D i s c u s s i o n - . *C. pusillus* is one of the commonest and most widespread species of the genus, though its distribution is narrower than that of other common species like *minutus* and *atratus*. In spite of its frequency and broad distribution *pusillus* appears to show reduced geographic variation. The most significant morphological deviation we observed refers to three samples listed in the material examined from Mato Grosso (a gyne, GERMAIN leg., NHMB), Mato Grosso do Sul (Corumbá, 6 workers, 1 soldier, Silvestri, MCZC, NHMB), between Bayova and Guagua in Bolivia (6 workers, 1 soldier, LIZER & DELÉTANG, NHMB). Together with a certain geographical vicinity, these samples share a much more superficial sculpturation and shining coloration. They might be specifically separate from *pusillus*, though we prefer not to separate them formally from *pusillus* until more material will be available.

FERNÁNDEZ et al. (1996) report this species also from the Colombian state of Bolívar.

D i s t r i b u t i o n : Colombia, Venezuela, Trinidad, Guyanas, Ecuador, Peru, Bolivia, Brazil, Argentina, Paraguay.

5.6.4. The *solidus* clade

This clade contains a single species – *solidus* – known from five workers only. Several important male, gyne and soldier characters remain unknown and we may expect the phylogenetic position of this species to be subject to considerable change once soldiers, gynes and males will be discovered. The sole apomorphy of the clade resulting from our data matrix is the propodeum with basal and declivous faces not separate by a spine (char. 46, state 0), a character state common to all most specialised species of the genus and regularly absent in the clades topologicaly closer to *solidus*. Other autapomorphies of *solidus* that we consider of lesser importance are listed under the species' treatment. KEMPF (1974) considered *solidus* as a member of his (1958 a) "*angustus* group", corresponding *grosso modo* to the three terminal clades of our phylogeny. All members of the "*angustus* group" (and other species as well) exhibit the same propodeal morphology as *solidus* and confirm, in this way, KEMPF's intuitive placement of this species. In addition, most critical synapomorphies for the clade better corresponding to Kempf's "*angustus* group" in our phylogeny are soldier or gyne characters, i. e. characters unknown in *C. solidus*. *Solidus*, however, lacks a number of worker synapomorphies of different hierarchic level regularly present among most members of the "*angustus* group". The most significant ones are probably characters 39–42 state 1 (*solidus* = 0).

By means of the CONSTRAINTS command of PAUP we forced *solidus* to into a clade corresponding to KEMPF's "*angustus* group". All 14 resulting possible optimal trees are only two steps longer than our phylogeny of Fig. 24. The position of *solidus* is constant in all 14 trees: it results as the outgroup species of all the other members of KEMPF's "*angustus* group".

Cephalotes solidus (KEMPF) new combination
Fig. 71

Zacryptocerus solidus KEMPF, 1974: 73, figs. 3, 4. Worker. Original description. Type locality: Colônia Santo Antonio (Manaus, Brazil). Type material: Holotype (unique) worker labelled: " Manaus, AM, Col. Santo Antonio, II-VI–1971, INPA # 16, Holotypus", in MZSP (examined).

D i a g n o s i s . - An isolate species representing a clade of its own for the broad and round vertexal angles, for the humeral angles with a short spine, and for the mesonotum and propodeum unarmed.

W o r k e r (Fig. 71) (description of KEMPF, 1974). - "Total length 5.4 mm; head length 1.49 mm; head width (eyes included) 1.81 mm; interocular width (maximum width of head between upper border of eyes) 1.62 mm; maximum diameter of eyes 0.46 mm; Weber's length of thorax 1.57 mm; maximum width of pronotum 1.35 mm; hind femur length 1.00 mm; petiole width 0.65 mm; sagittal length of gaster 1.75 mm; width of gaster 1.70 mm. Black, tip of mandibles, frontal carinae (in part), tibiae (except fuscous flexor face of mid and hind tibiae), tarsomeres, and anterolateral border of gaster ferruginous; tip of apical funicular segment pale yellowish brown. Integument opaque, finely reticulate-punctate throughout, with superimposed reticulate-rugose macrosculpture which is very distinct posteriorly and postero-laterally on dorsum of head, on cheeks, on dorsum and sides of thorax (the horizontally coarsely costate sides of pronotum excluded) on dorsum of petiole and postpetiole, on apical half of extensor face of all femora, on extensor face of tibiae; the same reticulate-rugose sculpture is slightly more superficial on tergum I of gaster, and vestigial to obsolete on remaining parts of the body and appendages; underside of the gaster laterally finely longitudinaly

rugose, the rugae curving mesad in front, lacking entirely on disc of sternum I; mandibles longitudinally costate-rugose; declivous face of propodeum coarsely longitudinally costate. Common, pointed erect to suberect hairs abundant on mandibles, shorter and scarcer on funiculus of antennae which also bear dense appressed pubescence. Short, thick, erect and-apically blunt setae scarce, on anterior and lateral margin of frontal carinae, above eyes, on tip of lateral pronotal and petiolar and postpetiolar spines, on tip of femora and tibiae. Remaining hairs scalelike, golden, glittering, appressed and mostly canaliculate, abundant on dorsum of head, dorsum and sides of thorax (except the glabrous sides of pronotum), on dorsum of petiole and postpetiole, on apical half of extensor face of femora and on entire extensor face of tibiae, on dorsum of gaster; very dense, masking entirely the integument, on cheeks which appear plated with gold; rare, simple not canaliculate golden hairs on gular face, on sides and flexor face of femora and tibiae and on sternum I of gaster. Laterotergite of pronotum, declivous face of propodeum, and anterior face of petiole, underside of petiole and postpetiole glabrous. Anterior border of clypeus with the usual comb of dense hairs projecting over the mandibles.

Head broader than long, with strongly anteriorly converging frontal carinae. Clypeal suture vestigial. Sides of head scarcely upturned above eyes. The latter very large, measuring nearly one third of head length, the anterior orbit reaching the middle of head length. Occipital lobes solid, not foliaceous nor platelike, but with sharply carinate border. Cheeks sharply marginate below. Dorsum of head very gently curved longitudinally, nearly straight and flat transversely. Pronotum anteriorly distinctly marginate, the scapular corners distinct, projecting, visible from above, the sides with a strong projecting first tooth, the second tooth at best vestigial, the third entirely absent. Promesonotal suture distinct but not conspicuous. Mesonotum laterally unarmed and entirely immarginate. Metanotal suture impressed. Basal face of propodeum likewise unarmed and practically immarginate on sides; declivous face slightly excavated on disc, the sides submarginate. Femora, especially hind femora, not slenderly fusiform but compact, the extensor face, seen in profile is strongly convex and almost angulate in the middle. Petiole with an oblique anterior face, noticeably distinct from the dorsal surface, the sides with a prominent, stout denticle. Postpetiole longitudinally flat, transversely convex, the lateral appendages longer, with a subacute tip. Tergum I of gaster anterolaterally with a platelike prominent margin, which is subtransparent but much narrower than the length of the postpetiole, reaching back on sides of gaster to the vestigial dorsal stigma; anterior half of sides of gaster sharply emarginate, posteriorly half rounded."

Measurements (in mm) and indices: TL 5.26–5.56; HL 1.28–1.32; HW 1.64; EL 0.44–0.45; PW 1.28; PeW 0.56–0.60; PpW 0.60–0.63; HBaL 0.51–0.52; HBaW 0.15–0.16; CI 124.2–137.0; PI 128.1; PPeI 213.3–228.6; PPpI 203.2–213.3; HBaI 29.4–30.7.

Material examined. - **Brazil**: Amazonas: Manaus, Colônia Santo Antônio, 1 worker (holotype) [MZSP]; Reserva Flor. A. Ducke, 2°55' S, 59°59' W, terra firme, 16.II.1982, 2 workers, Adis et al. [INPA]. Acre: Cruzeiro do Sul, 07.VI–14.VII 1983, 2 workers, R. H. Pires [MZSP].

Discussion. - *C. solidus* is an isolated species, not fitting into any of the other clades resulting from our cladistic analysis. Its combination of characters like round vertexal angles, short pronotal spines, absence of mesonotal spines, hind femora weakly angulated, and unarmed propodeum contribute to its isolate position within the *Cephalotes* phylogeny. Kempf (1974) suggested that *solidus* should belong to his *angustus* group while in our cladistic analysis it appears between *duckei* and the *pusillus* clades. We would like to add other, intuitive, arguments supporting the results of our cladistic analysis. The superficial reticulation on the ventral part of the head of *solidus* and its flat mandibles make this species much closer to members of the neighbour *laminatus* and to some species of the *basalis* clade than to the members of the *angustus* clade.

Distribution: Brazil.

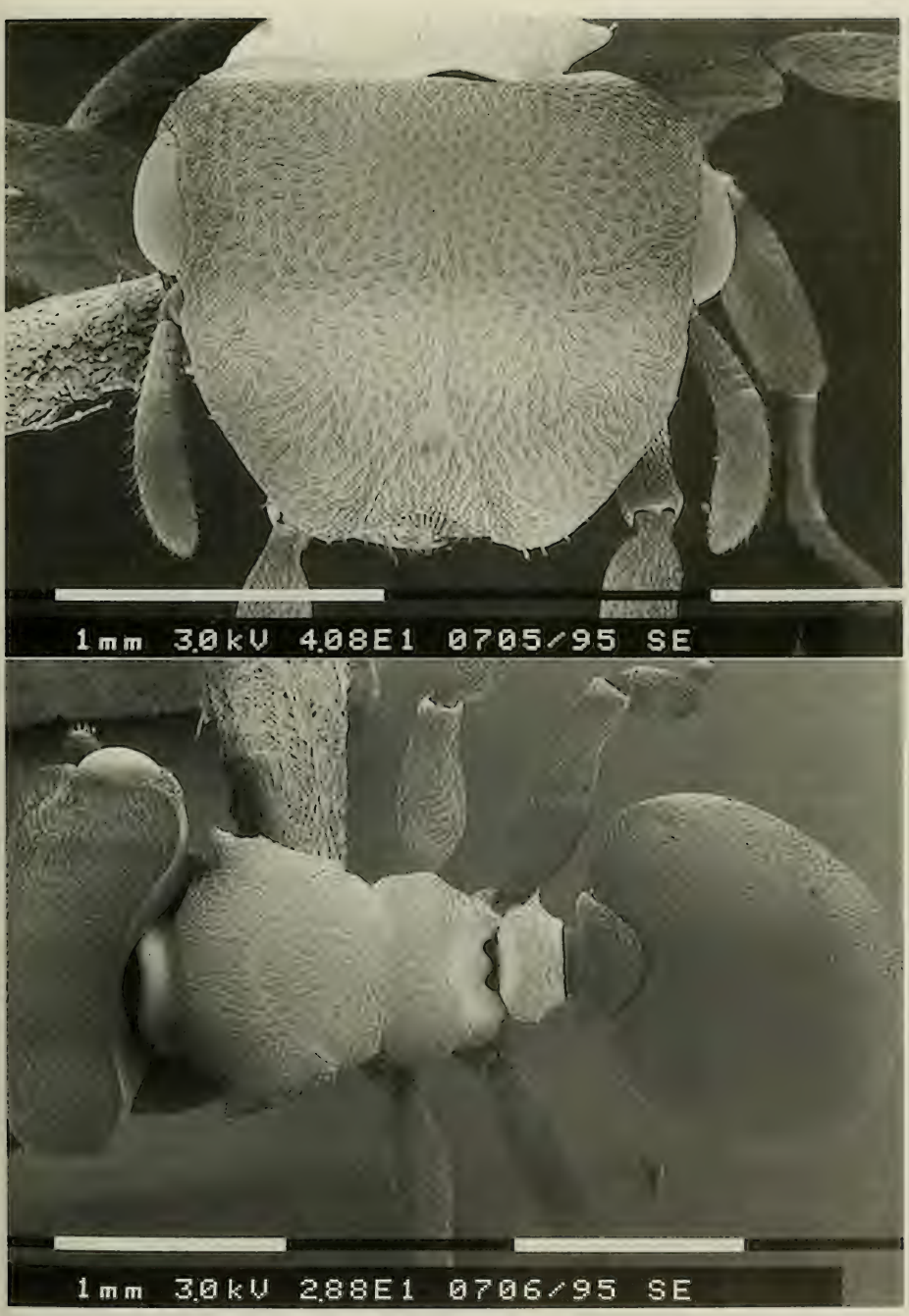


Fig. 71. *Cephalotes solidus* (KEMPF). Worker from Cruzeiro do Sul (Acre), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

5.6.5. The *laminatus* clade

A medium size clade containing seven Recent species characterised by the following synapomorphies: vertexal angles of the worker with a truncate lamella and gyne with four coloured spots on the gaster, a character which appears to have been secondarily lost in *christopherseni*; in this species the four coloured gastral spots are still visible as an undifferentiated macula in some specimens. Most species of the clade appear to be restricted to the S American rain forest with the remarkable exception represented by *minutus* which is one of the commonest and most broadly distributed species of the genus. This clade corresponds roughly to KEMPF (1951) "*spinosus* group" with his 1974 addition of *duckei*.

Species included in the clade: *christopherseni*, *duckei*, *inaequalis*, *laminatus*, *minutus*, *simillimus*, *spinosus*.

Cephalotes duckei (FOREL) new combination

Figs. 72, 73, 74, 75, 76, 77

Cryptocerus duckei FOREL, 1906: 233. Small soldier. Original description. Type locality: Barcelos (Amazonas, Brazil). Type material: lectotype and paralectotype intercastes labelled " Barcellos, 2.7.1905, A. Ducke; *Cr. Duckei* Forel, worker type, Rio Negro, Amazonas (Ducke); *P. duckei* For. uppermost soldier Lectotypus WWK", in the MHNG (KEMPF, 1967: 363) (examined).

Zacryptocerus duckei (FOREL), KEMPF, 1974: 69, fig. 1. Worker. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *laminatus* clade differing from all the other species of the clade in the worker and in the soldier by the rectangular pronotal lamellae and the angulate hind femora, and in the soldier and in the gyne by the presence of an incomplete disc.

W o r k e r (Fig. 72) (description of KEMPF, 1974). "Total length 3.7–4.3 mm; head length 1.11 – 1.28 mm; interocular width (distance between the inner borders of the eyes across the head) 1.13 – 1.35 mm; maximum diameter of eyes 0.27 – 0.30 mm; Weber's length of thorax 0.97 – 1.10 mm; pronotum width (projecting flange included) 1.03 – 1.19 mm; petiole width 0.45 – 0.54 mm; postpetiole width 0.39 – 0.54; gaster width 1.37 – 1.51 mm. Dorsal outline of body shown in Fig. 1. Exactly like the types (aborted soldiers) with the following differences: Head slightly narrower but still broader than long; occipital flanges more projecting and semidiaphanous. Scapular corners acute. Lateral projection of pronotum apically bidentate, foliaceous and semidiaphanous. Transverse pronotal carina absent (the large specimens of the series already have vestiges of a transverse carina in the form of a pair of minute denticles on pronotum). Tips of propodeal, petiolar and postpetiolar spines likewise depigmented and light in color."

Measurements (in mm) and indices: TL 3.84–4.60; HL 0.95–1.08; HW 1.28–1.48; EL 0.28–0.30; PW 1.04–1.20; PeW 0.49–0.56; PpW 0.45–0.50; HBaL 0.36–0.44; HBaW 0.11–0.13; CI 134.7–137.0; PI 123.1–123.3; PPeI 212.2–214.3; PPpI 231.1–240.0; HBaI 29.5–30.5.

S o l d i e r (Fig. 73) (previously undescribed). - Head feebly convex. Frontal carinae converging before the eyes and prolonging behind the eyes as a margin. Vertexal angles obtuse. Vertex with a pair of median short teeth connected each other by a median carina continuing laterally to join the frontal carinae. Mandibles broad, with a small lateral tumulus.

Mesosoma. Scapular angles short. Humeral angles with a broad lateral lamella, with pointed anterior border followed by a concavity and a subround, obtuse tooth, and posteriorly converging sides. Pronotal carina wide, interrupted in the middle by a deep notch. Promesonotal suture impressed on the sides. Mesonotum with a broad, rounded tooth. Propodeal suture deeply impressed. Propodeum clearly differentiated in basal and declivous faces. Basal face with three pairs of teeth; the anterior one, small, broad and subtriangular, the

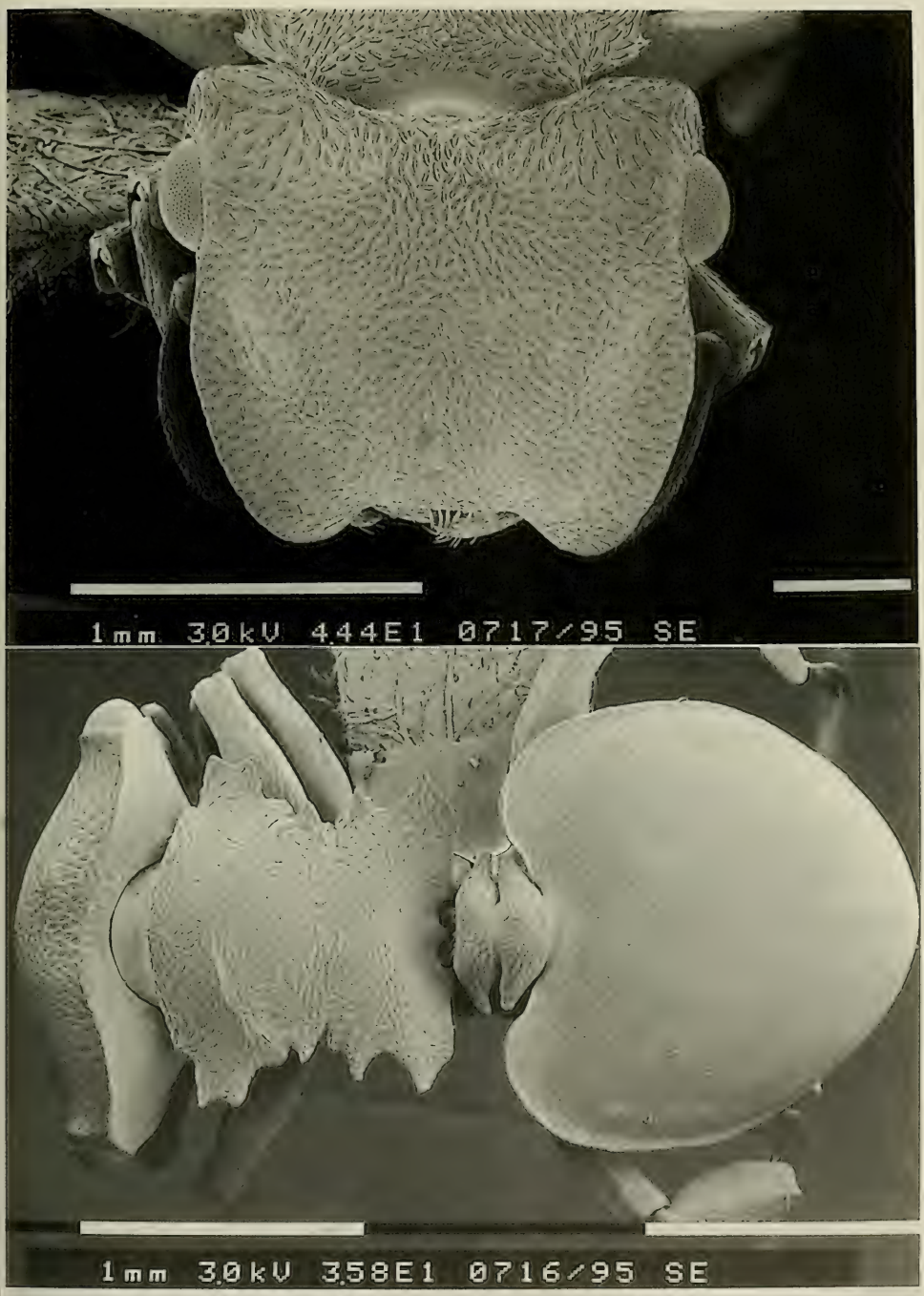


Fig. 72. *Cephalotes duckei* (FOREL). Worker from Reserva La Macarena, Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 73. *Cephalotes duckei* (FOREL). Soldier from Mato Grosso, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

median one small and high, and the posterior pair broad, subpointed, lamellaceous and converging towards the declivous face.

Petiole with the anterior border slightly concave; petiolar spines directed backwards and with round tips. Postpetiolar spines as in the petiole, but originating on the anterior face of the postpetiole and curved laterally.

Gaster oval, with a broad lamellaceous border reaching the stigma and continuing backwards as a thin margin.

Legs. Fore coxae with a broad lobe anteriorly. Mid and hind femora forming an angle without denticles. Hind basitarsi flat and broad at the base.

Sculpture. Head dorsum minutely reticulate-punctate and covered by faint, small oval foveae with their interspaces larger than maximum fovea diameter; this sculpture more superficial on the frontal carinae. Vertexal area behind the head disc, ventral part of the head, mesosoma and pedicel reticulate-punctate and foveolate, the foveae larger and deeper than those on the head dorsum, shallower on the basal face of the propodeum and on the pedicel, sparser on the propleurae. Declivous face of the propodeum, meso- and metapleura, legs and gaster reticulate-punctate. Posterior half of the first gastral sternite centrally faintly reticulate-punctate, almost shining.

Pilosity. Each fovea bears a thick, appressed, canaliculate hair; gaster and legs with sparse hairs, thinner than those on the pronotum. Mandibles, legs and posterior part of gaster with slightly clavate, suberect hairs, longer on the gaster. Cheeks without appressed hairs.

Colour. Head, mesosoma and basitarsi dark brown. Frontal carinae, pedicel and legs ferrugineous. Gaster reddish to light brown.

Measurements (in mm) and indices: TL 6.24–6.72; HL 1.48–1.64; HW 2.00–2.08; EL 0.40; PW 1.88–2.04; PeW 0.73–0.80; PpW 0.70–0.72; HBaL 0.56–0.60; HBaW 0.20; CI 126.8–135.1; PI 101.9–106.4; PPeI 255.0–257.5; PPpI 268.6–283.3; HBaI 33.3–35.7.

G y n e (Fig. 74) (previously undescribed). - Head with traces of disc, dorsally convex. Frontal carinae convex anteriorly; their sides converging in front of and ending behind the eyes. Vertexal angles round. Vertex with a pair of median teeth connected each other by a median carina continuing laterally to junction of the mandibles.

Mesosoma. Humeral angles with a pointed anterior tooth. Pronotal crest narrow and superficially interrupted in the middle. Mesonotum and scutellum flat. Lower mesopleura with a small denticle.

Basal face of propodeum with two broad and round teeth, the anterior smaller than the posterior ones, the latter between the basal and declivous faces; declivous face concave.

Petiole with the anterior border slightly concave and oblique; petiolar sides convex, without spines. Postpetiole broadly convex; anterior sides of the postpetiole with a small, obtuse tooth or unarmed.

Gaster with a broad anterior lobe.

Legs. Fore coxae with a broad lobe anteriorly. Mid and hind femora not angulate. Hind basitarsi flat and slightly broadened at their base.

Wings (Fig. 75). Fore wings with *R+Sc* superficially connected with a marked pterostigma. *2r* marked, *Rsf5* connected with *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; *CuA*, *M* and distal part of *1A* vestigial.

Sculpture. Head minutely reticulate-punctate and covered by faint, small foveae with their interspaces larger than their maximum diameter. Frontal carinae with foveae sparser than those on the head and superficially reticulate-punctate almost shining. Occipital area behind the head disc, ventral part of the head, mesosoma, pedicel reticulate-punctate and with foveae larger and deeper than those on the head dorsum; the foveae sparser on the anterior half of the propleurae and on the middle of the mesopleurae and on the pedicel dorsum, denser, deeper on the propodeum, over the metapleural gland. Concavity of the declivous face of the propodeum, anterior third of the mesopleurae, area under the metapleural gland, legs and gaster reticulate-punctate. Shallower reticulation on the legs and on the gaster, slightly shining. First gastral sternite faintly reticulate-punctated almost shining, centrally and posteriorly.

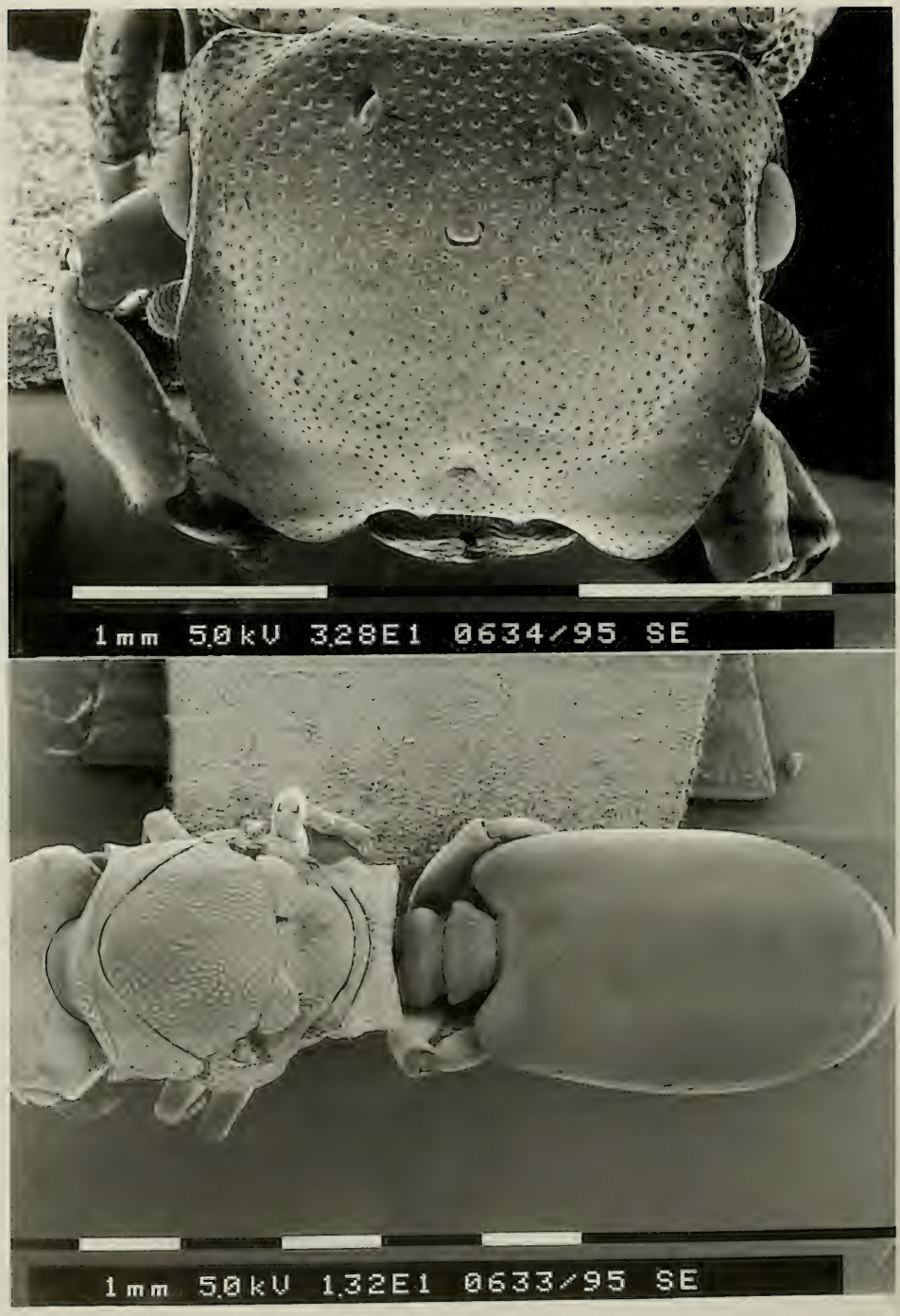


Fig. 74. *Cephalotes duckei* (FOREL). Gyne from Reserva La Macarena, Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 75. *Cephalotes duckei* (FOREL). Gyne from Reserva La Macarena, Colombia, fore and hind wings.

Pilosity. Each fovea bears a thick, appressed, canaliculate hair; mandibles, mesosoma, pedicel and legs with rare, slightly clavate, suberect hairs, longer and sparser on the apex of the gaster. Legs and gastral sternites with sparse and thinner hairs than those on the foveae.

Colour. Head, mesosoma, pedicel and basitarsi dark brown, frontal carinae and legs lighter. Gaster reddish to light brown, with two pairs of yellow spots, one on the gastral lobes and the other pair on the posterior sides of the first gastral tergite.

Measurements (in mm) and indices: TL 11.04–11.36; HL 2.04–2.12; HW 2.36; EL 0.44–0.48; PW 2.28–2.32; PeW 0.96–1.00; PpW 0.88–1.00; HBaL 0.72–0.75; HBaW 0.26–0.28; CI 113.2–115.7; PI 103.4–105.3; PPeI 228.0–241.6; PPpI 228.0–272.7; HBaI 34.6–38.8.

M a l e (Fig. 76) (previously undescribed). - Head (eyes included)1/3 broader than long; sides of the head convex, converging to the straight vertexal margin. Vertex dorsally protruding, bearing salient ocelli. Compound eyes broadly convex, in the middle of the sides of the head. Frontal carinae diverging backwards, not reaching the median ocellus posteriorly. Frons flat. Clypeus slightly convex; its posterior border marked by a convex carina; its anterior border with a median concavity between a pair of small denticles absent in some specimens. Mandibles slim, with a pointed apical tooth followed by 4–5 minute denticles; external face without carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints filiform and thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards, without carinae. Mesonotal scutum convex in side view; median Mayrian furrow little impressed. Scutellum convex, its sides converging posteriorly. Basal and declivous faces of the propodeum poorly

Fig. 76. *Cephalotes duckei* (FOREL). Male from Reserva la Macarena, Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

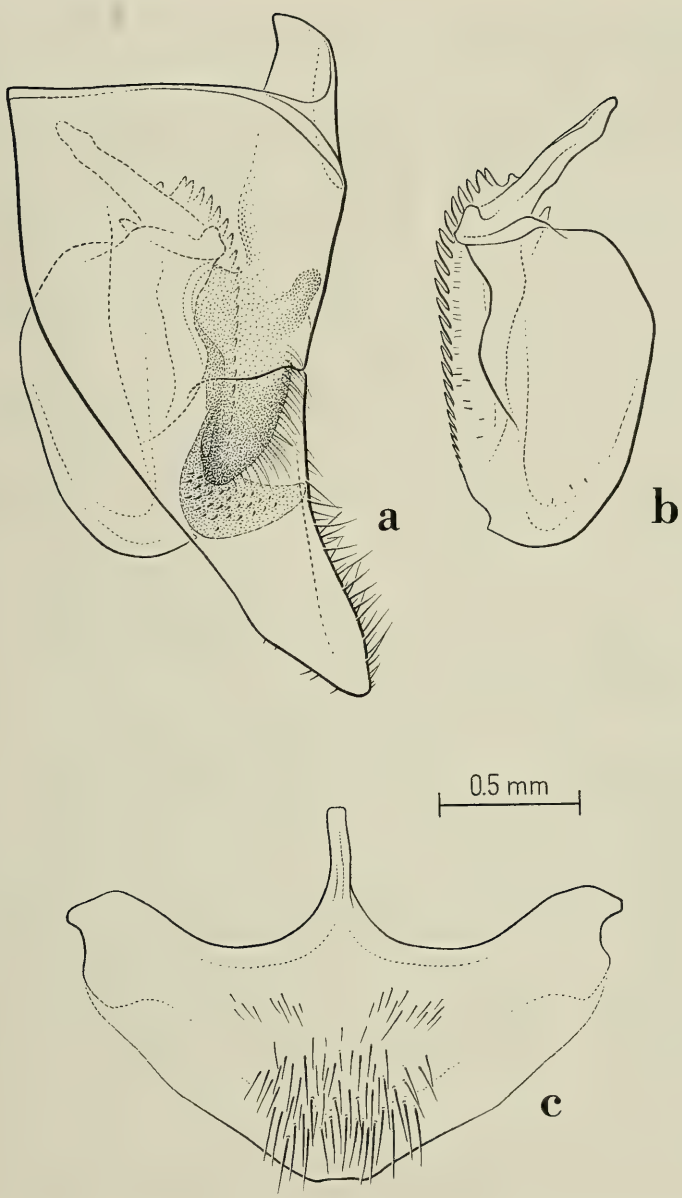


Fig. 77. *Cephalotes duckei* (FOREL). Male from Reserva La Macarena, Colombia. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

differentiated; basal face little sloping and convex; declivous face shorter than the basal one and almost straight. Propodeal sides marked by a longitudinal, convergent carina.

Petiole narrower than the postpetiole. Anterior face of the petiole oblique and medially concave; posterior face flat. Petiolar sides convex anteriorly, converging posteriorly. Postpetiole little convex dorsally; its sides with a subround tooth.

Gaster as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 77.

Wings. As in the gyne.

Sculpture. Head dorsum reticulate, irregularly rugulose, with dense foveae on the vertexal border and sparse foveae on the frons. Ventral face of the head, lower mesopleurae, upper metapleurae, basal face and anterior half of the declivous faces of the propodeum, and sides of the petiole longitudinally rugulose. Mesonotum, scutellum, propleurae and upper mesopleurae superficially reticulate-foveolate. Postpetiole, first gastral tergite and sternite reticulate, remaining gastral segments and legs superficially reticulate and slightly shining.

Pilosity. Body with three types of hairs: (1) flexuous, long, thin, pointed hairs dense on the head, the mesosoma, the pedicel and the legs, slightly sparser on the gaster; (2) shorter than the cephalic hairs, decumbent, dense on the anterior border of the pronotum and on the dorsum of the petiole, and sparser on the outer face of the femora and on the postpetiolar dorsum; (3) short, appressed and suberect on the funiculi.

Colour. Head, mesosoma, pedicel and coxae dark brown to black; antennae lighter. Gaster, legs and wings yellow to light brown, wings slightly infuscated; tarsi reddish brown. Body hairs golden.

Measurements (in mm) and indices (based on two specimens from Reserva La Macarena, Meta, Colombia): TL 9.24–9.56; HL 1.08–1.16; HW 1.48; EL 0.48–0.50; PW 1.88–2.00; PeW 0.72–0.76; PpW 0.90–0.92; HBaL 0.92; HBaW 0.16; CI 127.6–137.0; PI 74.0–78.7; PPeI 261.1–263.1; PPpI 208.8–217.4; HBaI 17.4.

Material examined. - **Colombia**: Meta: La Macareña, Caño La Curia, 20.XII.1986, 1 soldier, D. Rivers [MZSP]; Res. Nat. La Macareña, Caño La Curia, Est. las Dantas, VII.1987, 1 soldier, 1 gyne, D. Rivers [MZSP]; Reserva La Macareña, Est. Las Dantas, INDERENA, Caño La Curia, 580 m, 09.VIII.1987, 6 workers, 2 small soldiers, 2 gynes, 3 males, D. Rivers & F. Fernandez [LACM].

Brazil: Amazonas: Barcelos, 02.VII.1905, 2 small soldiers (lectotype and paralectotype) [MHNG]; Reserva Flor. A. Ducke, 2°55' S, 59°59' W, terra firme, 21.VIII.1991, 9 workers, Adis et al. [INPA]; same locality and collectors, 26.VII.1994, 5 workers; same locality, 24.I.1996, 1 gyne, M. L. de Andrade [INPA]. Pará: Boca do Cuminá-Miri, Oriximiná, I.1968, 21 workers, Exp. Perm. Amaz. [MZSP]; Serra Norte, Manganês, 24.VI.1986, 1 worker, M. F. Torres [MPEG]. Mato Grosso: Vila Vera, X.1973, 4 workers, M. Alvarenga [MZSP]; Sinop, 55°37' W 12°31' S, X.1974, 17 workers, 14 soldiers, 1 gyne, M. Alvarenga [MZSP]; Sinop, 55°37' W, 12°31' S, II.1976, 1 worker, O. Ropa [MZSP].

Discussion. - Kempf (1974) makes a detailed discussion of the probable phylogenetic position of *duckei* with which we agree entirely and which is confirmed by the results of our cladistic analysis. This species appears to be rare in the collections, even in those from intensely collected areas, like the Reserva Ducke in Amazonas.

Distribution: Colombia and Brazil.

Cephalotes minutus (Fabricius) new combination

Figs. 78, 79, 80, 81, 82, 83

Cryptocerus minutus Fabricius, 1804: 420. Worker. Original description. Type locality "in America meridionali", actually Essequibo (Guyana). Type material: 2 syntype workers in ZMUC (Zimsen, 1964: 427) (examined), only one of which labelled "Essequibo, Smidt, Mus. de Sehestedt, *Cryptocerus minutus* Fabr.".

Cryptocerus quadrimaculatus Klug, 1824: 215. Gyne. Original description. Type locality: Pará (Brazil). Type material: not available for the present study. Synonymy by Emery, 1890: 74.

Formica caustica Kollar, 1832, in Pohl & Kollar, 1832: 17, fig. 12. Worker. Original description. Type locality: Brazil. Type material: not available for the present study. Synonymy by Emery, 1890: 74. Note: synonym of *pusillus* in Emery (1922) and Kempf (1951).

Cryptocerus cognatus SMITH, 1862: 411, pl. 13, fig. 4. Gyne. Original description. Type locality: Ega (= Tefé), Amazonas (Brazil). Type material holotype gyne (unique) labelled "Ega, Amazon." in BMNH, examined. New synonym.

Cryptocerus exiguus SMITH, 1867: 524. Worker. Original description. Type locality: Mexico. Type material: holotype worker (unique) labelled "Mex., *Cryptocerus exiguus*. Sm. Trans. Ent. Soc." in OXUM (Type Hymenoptera 1044) (KEMPF, 1958 b), examined. Synonymy by KEMPF, 1958 b: 110.

Cryptocerus volxemi EMERY, 1878: 2. Worker. Original description. Type locality: Brazil. Type material: holotype worker labelled "Coll. Camille Van Volxem, Volxemi, Emery, Brasil" in MCSN, examined. Synonymy by EMERY, 1890: 74.

Cryptocerus minutus FABRICIUS, EMERY, 1890: 74. Male.

Cryptocerus minutus var. *cognatus* (sic) SMITH, EMERY, 1922: 307.

Cryptocerus minutus var. *cognatus* (sic) SANTSCHI, 1931 a: 275. Partim. Three syntype workers labelled: 1) "Panama, La Conception, 16.VII.30, Bierig"; 2) "Costa Rica, Mateo, Biolley, *Cryptocerus minutus*, F. *Cr. minutus* F. worker, El Hiquito p. San Mateo (Costa Rica), Tronc et feuilles de *Bixa orellana*, (Biolley). *Cr. minutus v. cognatus* Sm"; 3) "Museum Paris, Rives De L' Amazone, Stevens 1855, *Cryptocerus minutus* F., Santschi det. 1921, *Cr. minutus* v. *cognatus* Sm"; all in NHMB, examined. Misidentification. Nec soldier.

Paracryptocerus minutus (FABRICIUS), KEMPF, 1951: 169, figs. 122, 123. Worker, soldier, gyne. First combination in *Paracryptocerus*.

Paracryptocerus minutus (FABRICIUS), WHEELER & WHEELER, 1954 b: 155, figs. 31 – 38. First instar, young and mature worker larva.

Paracryptocerus cognatus (SMITH), KEMPF, 1958 a: 137. First combination in *Paracryptocerus*.

Zacryptocerus cognatus (SMITH), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

Zacryptocerus minutus, KUGLER, 1978: 474, fig. 199. Worker, sting. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *laminatus* clade characterised in the worker by the eyes having a maximum diameter greater than 1/3 of the head length, and, in the worker and in the soldier, by the propodeal spines not expanded ventrally into a lamella.

Worker (Fig. 78) (description of KEMPF, 1951). - "Length 3.4 mm. Median head length 0.88 mm; Weber's length of thorax 0.95 mm. Black; the following light reddish-brown: antennae, tips of mandibles, tips of femora, tibiae, tarsi, apical half of basitarsus, apices of first prothoracic tooth, epinotal and peduncular spines, anterolateral border of gaster, distal border of gastral tergites and sternites. Frontal carinae and upper face of tibiae pale yellowish.

Head opaque; slightly longer than broad, broadest behind the eyes; interocular distance somewhat shorter than the maximum length of the head (43:40). Lateral margins of head scarcely sinuate above the eyes. Posterior margin straight mesially, the occipital angles with slightly projecting, subtransversely truncate, partly infuscated, lamellae, the apical border of which is more or less straight. Cheeks strongly marginate beneath, densely covered with flat, appressed silvery hairs. Eyes large, their longest diameter more than 1/3 of median head length. Upper and lower surface of head finely reticulate-punctate, sparsely covered with silvery, slender, simple, flat, scale-like, appressed hairs; slightly larger, denser, and somewhat canaliculate, lying in grooves, in front of the occipital border.

Thorax opaque. Anterior border moderately arcuate; shoulders sharply angulate. Pronotum somewhat expanded laterally behind the shoulders, with two short teeth on each side, the posterior tooth slightly shorter than the anterior. Posterior corners of pronotum projecting, forming a rectangular tooth. Promesonotal suture vestigial laterad, obsolete mesad. Mesonotum on each side with a small, acute, projecting tooth. Mesoepinotal suture not deeply impressed, more or less vestigial. Basal face of epinotum with an anterolateral, smaller recurved spine and a posterior long, slender spine, twice as long as the first, greatly divergent, more than 45° from the longitudinal axis. Declivity not excavated, its sides not conspicuously crested, but finely longitudinally striated, without scales. The entire thorax finely reticulate-punctate, the upper face very little convex longitudinally and transversely, with rather dense,

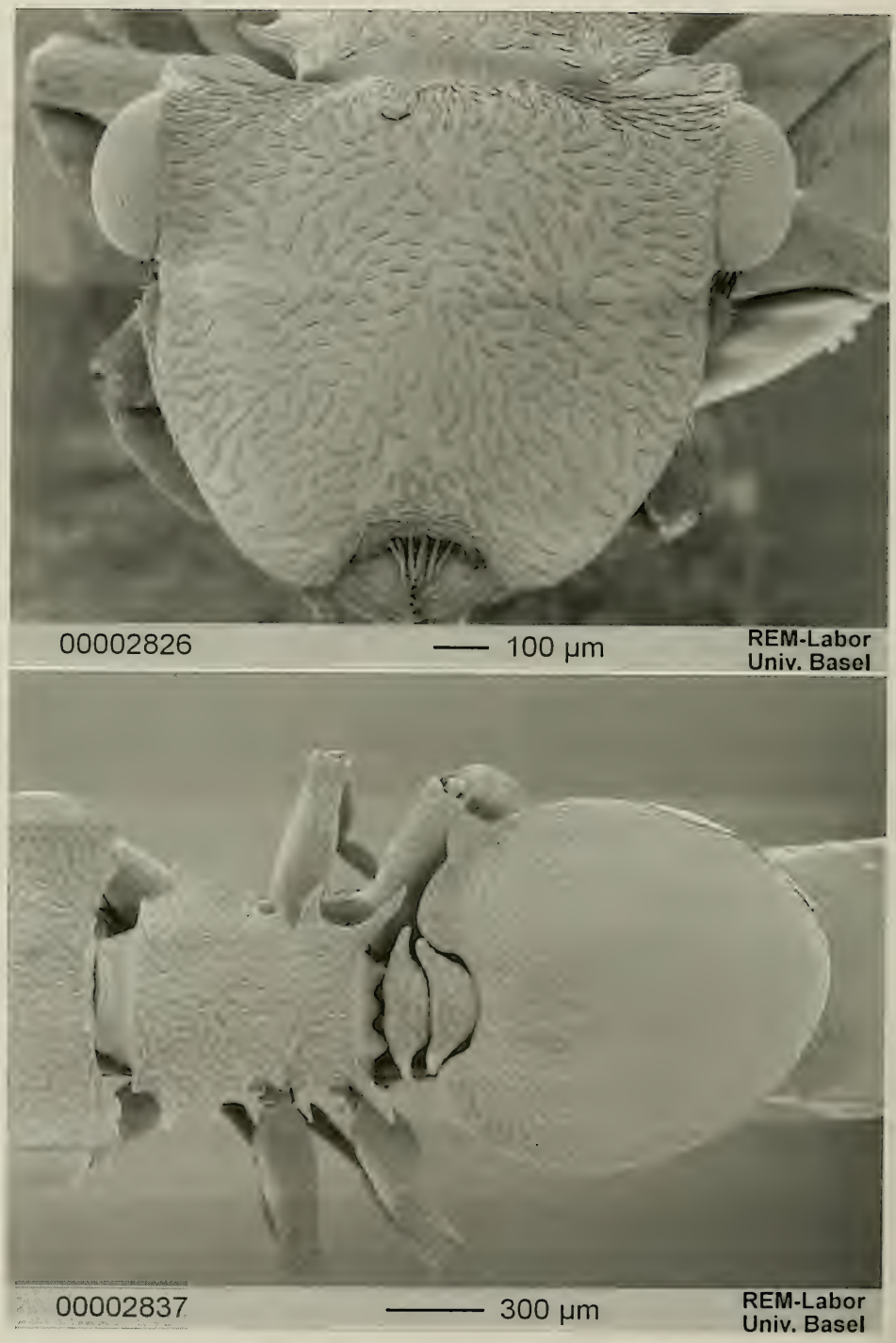


Fig. 78. *Cephalotes minutus* (FABRICIUS). Worker from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

more or less longitudinal, elongate grooves, each containing a flat, canaliculate, appressed silvery scale. Laterotergite of pronotum and mesopleura longitudinally striated, sparsely scaled.

Petiole opaque, transverse, with a long, subacute spine on each side. Postpetiole slightly longer than petiole, transverse, with a somewhat shorter, broader, spine, on each side, more or less rounded apically curving obliquely forward. Sculpture as on thorax, the sparse scales not lying in foveolae.

Gaster subopaque, somewhat elongate, depressed. First gastral tergite with rather narrow, not distinctly set off anterolateral lamellate border, emarginate mesad. Tergites and sternites finely reticulate-punctate. Scale-like silvery hair appressed, sparse and simple, not lying in deep foveolae. erect pile confined to apical half of first sternite and the exposed portion of the tergites 2–4 and the sternites."

Measurements (in mm) and indices: TL 3.12–3.82; HL 0.78–0.98; HW 0.94–1.16; EL 0.31–0.36; PW 0.75–0.96; PeW 0.47–0.58; PpW 0.42–0.48; HBaL 0.28–0.47; HBaW 0.06–0.07; CI 118.4–121.7; PI 120.8–124.4; PPeI 156.2–183.0; PPpI 178.6–195.6; HBaI 21.1–21.4.

S o l d i e r (Fig. 79) (description of Kempf, 1951). - "Length 7 mm. Median head length 1.90 mm; Weber's length of thorax 2.02 mm. Black; the following ferruginous: antennae, tip of femora, tibiae, tarsi. First gastral tergite with a large yellowish-brown spot on each corner.

Head subfulgid; slightly longer than wide (83:82). Frontal carinae arcuate, diverging caudad to above the posterior end of the antennal scrobe, where they form a distinct, very obtuse angle, and are prolonged in the form of a conspicuous, not raised margination above the eyes, fading out before reaching the posterior border of the eyes. Upper surface of head scarcely convex. Occiput sharply truncate, distinctly marginate on vertex. Occipital corners indicated by faint tubercular swellings on each side. Occipital border slightly convex. Cheeks immarginate below. Eyes flat. A distinct emargination extends from beneath the eyes back to the occipital corner. Upper surface of head finely punctate, with sparse, small foveolae, in which no distinct hair is visible. Foveolae slightly larger and more crowded on occiput, still larger, containing a distinctly visible, decumbent seta, on the lower surface of the head.

Thorax subfulgid above. Anterior border arcuate, shoulders subangulate. Sides of pronotum, with a strong lateral tooth, pointing obliquely forward. Transverse pronotal keel distinct, not sharply crested. Posterior corner of pronotum projecting in the form of a small rectangular tooth. In profile, the promesonotum is strongly convex. Promesonotal suture vestigial. Mesonotum with a stout, bluntly rounded, slightly upturned, marginate, lateral lobe. Thorax greatly constricted laterad between mesonotum and epinotum. Mesoepinotal suture impressed. Epinotum opaque. Basal face transverse with an anterolateral, broad, obtuse tooth, and a much stronger, greatly diverging posterior spine, with blunt apex, and a postero-ventral lamella, which does not border the declivity laterad. Declivous face longitudinally striato-rugose. Microsculpture of promesonotum as on head, epinotum and sides subopaque, reticulate-puncate. Upper surface of thorax foveolate, sparsely on the anterior portion of the pronotum, densely and deeply behind, the foveolae being much larger than those of the upper surface of head. Laterotergite of pronotum with sparse and more shallow foveolae.

Petiole opaque; transverse with a stout, short, subacute, somewhat recurved lateral tooth. Posterior half shallowly transversely concave. Postpetiole slightly longer than petiole, as wide as petiole, with a plate-like, apically subtruncate apical tooth on each side. Both segments finely reticulate-punctate.

Gaster subopaque; elongate, the anterior border emarginate mesad, anterolaterally strongly marginate, without a distinct lamellate border. Sides subparallel, scarcely convex. Tergites and sternites finely reticulate-punctate, without foveolae.

All foveolae, except the ones on the upper surface of head and promesonotum, bear a decumbent, flattened seta. Setae rather shiny on epinotum. Gaster with minute, shiny, scale-like scattered hairs. Erect pile confined to the terminal tergites and sternites of gaster and the posterior half of the first sternite."

Measurements (in mm) and indices: TL 5.30–6.92; HL 1.48–1.84; HW 1.60–1.80; EL 0.42–0.44; PW 1.30–1.64; PeW 0.66–0.78; PpW 0.60–0.74; HBaL 0.40–0.46; HBaW 0.10–0.12; CI 97.6–108.1; PI 109.7–123.1; PPeI 185.7–212.1; PPpI 216.7–233.1; HBaI 25.0–27.6.

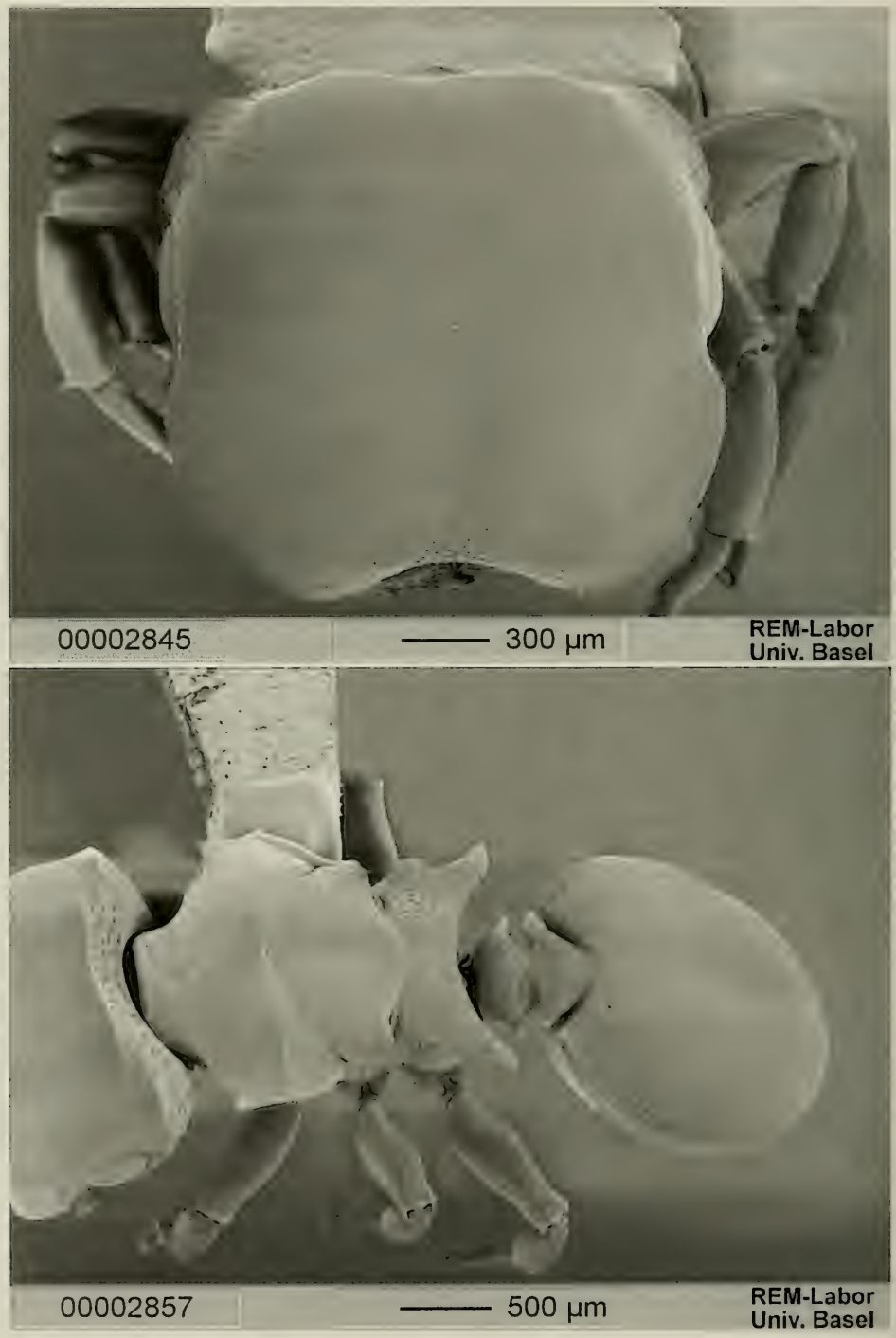


Fig. 79. *Cephalotes minutus* (FABRICIUS). Soldier from Honduras: head (top) and meso- and metasoma (bottom) in dorsal view.

G y n e (Fig. 80). – Head convex and without disc. Frontal carinae curved, reaching the anterior border of the eyes and converging posteriorly. Vertexal angles subround. Ocelli broad and deeply impressed. Eyes large and little convex, their anterior border making an anterior ridge delimiting the frontal carinae posteriorly. Clypeus ventrally prominent with the head in full dorsal view, emarginate in the middle of the anterior border, without lateral teeth. Mandibles broad, without lateral carina. Cheeks not carinate.

Mesosoma flat in side view. Humeral angles with a short, pointed anterior tooth. Pronotal carina narrow; in some specimens interrupted on the sides. Mesonotum and scutellum flat. Lower mesopleura with a pointed denticle. Basal face of propodeum with two pairs of teeth; those of the anterior pair angulate or round, smaller and broader than those of the posterior one; the second pair between the basal and declivous faces and with pointed tips.

Petiole differentiated in anterior and posterior faces; anterior face almost vertical; posterior face gently sloping backwards. Petiolar sides with a minute. Postpetiole broadly convex on the middle; postpetiolar spines placed anteriorly, broad, with truncate tip directed laterally.

Gaster anteriorly protruding and with a simple margin not reaching the first stigma.

Legs. Fore coxae with a broad lobe anteriorly. Mid and hind femora not angulate. Hind basitarsi slightly flat and without broad base.

Wings. Fore wings with *R+Sc* superficially connected to a marked pterostigma; *2r* marked, *Rsf5* connected with *R1*; distal parts of *A*, *Cu-A1* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and 1*A* marked; *CuA*, *M* and distal part of *1A* vestigial.

Sculpture. Head, mesosoma and pedicel superficially reticulate-punctate and covered by foveae. Head dorsum with small, well impressed foveae with their interspaces broader than their maximum diameter, shallower and sparser on the frontal carinae. Ventral part of the head, anterior half of the pronotum, mesonotum and propleurae with foveae larger than those on the head dorsum. Posterior half of the pronotum and scutellum with foveae denser than those on the mesonotum. Propodeum, except the two posterior thirds, upper mesopleurae and pedicel with deep, contiguous foveae, more superficial on the pedicel. Lower mesopleurae and metapleurae with sparse, superficial foveae. Lower metapleurae punctate and with few longitudinal rugosities. Two posterior thirds of the declivous face of the propodeum punctate and with superficial transversal rugosities. Gaster and legs reticulate-punctate, with minute, superficial foveae on the gaster only.

Pilosity. Each fovea bears an appressed, canaliculate hair. Mesosoma, pedicel, gaster and legs with erect, slightly clavate hairs, rarer on the mesosoma and pedicel, sparse on the gaster.

Colour. Black with lighter gaster and proximal part of the femora. Distal part of the femora and remaining parts of the legs light brown. Gaster with two broad pairs of yellow spots, one on the gastral lobes, and the other on the posterior sides of the first tergite.

Measurements (in mm) and indices: TL 8.16–9.44; HL 1.52–1.68; HW 1.52–1.74; EL 0.42–0.47; PW 1.36–1.56; PeW 0.64–0.75; PpW 0.84–0.97; HBaL 0.51–0.55; HBaW 0.14–0.15; CI 100.0–106.1; PI 107.9–113.5; PPeI 187.6–233.8; PPpI 156.7–175.8; HBaI 25.4–27.4.

M a l e (Fig. 81). - Head (eyes included) more than 1/3 broader than long. Vertexal angles with an irregular margin with or without an obtuse medial tooth. Vertex dorsally protruding, bearing salient ocelli. Compound eyes broadly convex, at mid head length. Frontal carinae very short and diverging backwards. Frons flat. Clypeus convex posteriorly and with bidentate anterior border. Mandibles short, without external carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards. Humeral angles with or without a pair of denticles of variable size. Mesonotum convex in side view; median Mayrian furrow variably impressed but always present. Scutellum convex, rounded posteriorly. Basal and declivous faces of the propodeum differentiate; basal face gently convex; declivous face with converging sides.

Petiole with truncate anterior face; posterior face sloping posteriorly. Petiolar sides either unarmed or with a pair of small median denticles. Postpetiole convex and sub hexagonal dorsally; its sides with a small, pointed or round median denticle.

Gaster as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 82.

Wings as in Fig. 83.

Fig. 80. *Cephalotes minutus* (FABRICIUS). Gyne from Honduras: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 81. *Cephalotes minutus* (FABRICIUS). Male from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

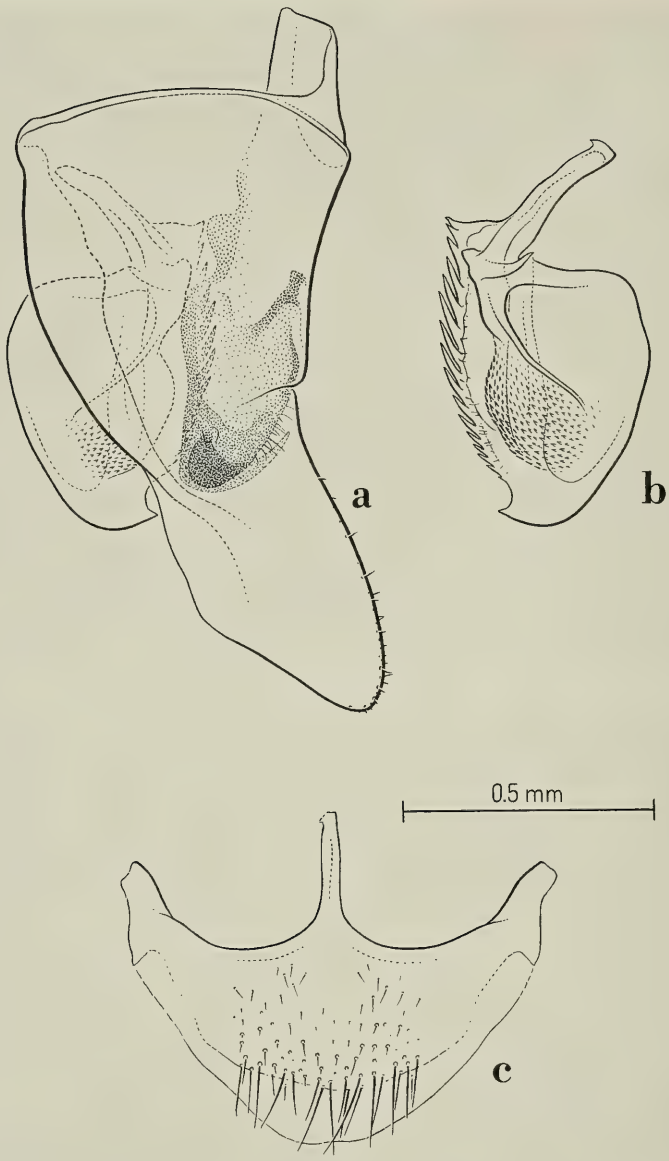


Fig. 82. *Cephalotes minutus* (FABRICIUS). Male from Manaus, Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Sculpture. Head dorsum minutely reticulate and irregularly rugose; this sculpture superimposed to superficial, variably clumped, irregular foveae on the vertexal area and frons. Ventral part of the head reticulate and with irregular foveae larger than those on the head dorsum. Pronotum, mesonotum, pro- and mesopleurae superficially reticulate-punctate and with few, very superficial and small foveae; scutellum reticulate and with foveae as on the mesonotum. Metapleurae and propodeum reticulate and with thin, longitudinal rugosities. Pedicel reticu-

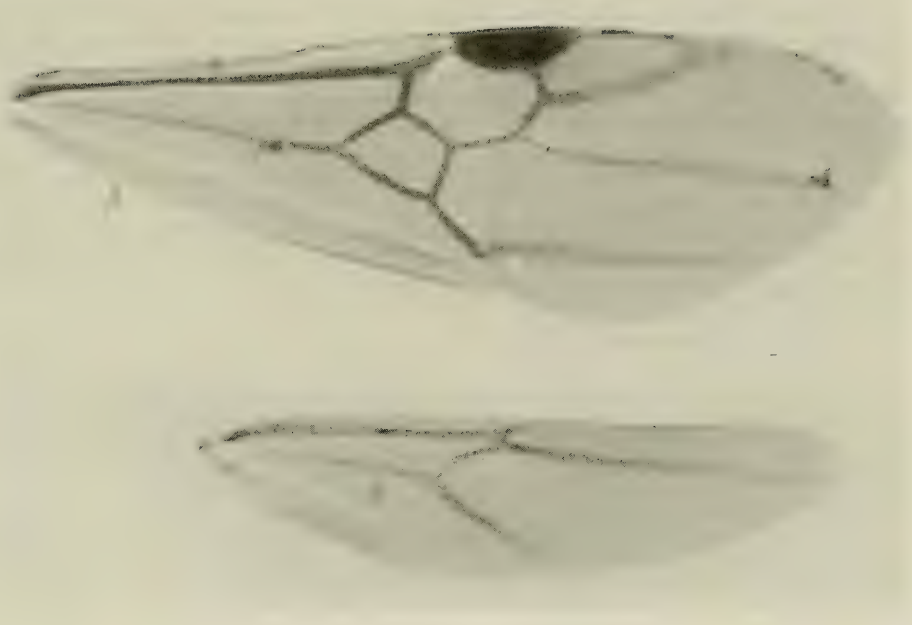


Fig. 83. *Cephalotes minutus* (FABRICIUS). Male from Manaus, Brazil, fore and hind wings.

late and with superficial, irregular foveae superimposed to weak, longitudinal rugosities on the sides only. First gastral tergite minutely reticulate; remaining tergites, sternites and legs superficially reticulate and weakly shining.

Pilosity. Body with long, thin, flexuous, pointed, golden hairs, dense on the head, on the mesosoma and on the pedicel, sparser on the gaster and on the femora. Gaster and legs with similar hairs but shorter, appressed on the tergites, decumbent on the sternites and on the femora. Tibiae and tarsi with short, pointed hairs.

Colour. Dark brown to black with lighter gaster. Coxae, proximal third to half of femora, tarsi dark ferrugineous to brown, remaining parts of the legs yellow.

Measurements (in mm) and indices: TL 5.64–6.00; HL 0.84; HW 1.04–1.08; EL 0.39–0.41; PW 0.88–0.92; PeW 0.52–0.54; PpW 0.60–0.68; HBaL 0.58–0.63; HBaW 0.09–0.10; CI 123.8–128.6; PI 113.0–122.7; PPeI 169.2–170.4; PPpI 139.4–146.7; HBaI 15.5–15.9.

Material examined. - **Mexico**: San Luís Potosí: 22 mi N of Tamazunchale, 05.I.1952, 2 workers, 1 soldier, W. S. CREIGHTON [MZSP]; 13 km N of Tamazunchale, 220 m, 08.VI.1988, 1 worker, 1 soldier, 1 gyne, 1 male, W. MACKAY [MHNG]; Tamazunchale, 03.IV.1953, 1 worker, 1 soldier, 1 gyne, 1 male, in rotten limb, W. S. CREIGHTON [MZSP]. Tamaulipas: 5 miles W of Altamíra, 22.IV.1950, 1 worker, 1 soldier, 1 gyne, in rotten limb, W. S. CREIGHTON [MZSP]; Tampico, 1912, 3 workers, E. A. SCHWARTZ [USNM]. Vera Cruz: Tamos, 07.XII.1909, 2 workers, F. C. BISHOP [USNM]; Pueblo Nuevo, nr. Tetzonapa, 12.VIII.1953, 6 workers, 15 soldiers, E. O. WILSON [MCZC]; El Palmar, 13.VI.1948, 4 workers, NUTTING & WERNER [MCZC]; Vera Cruz, 01 & 28.IV.1896, 19 workers, 1 soldier, TOWNSEND [USNM]; same locality, I.1959, XII.1961, XI.1963, XII.1969, 11 workers, N. L. KRAUSS [USNM]; Palma Sola, 28.V.1972, 1 worker, P. REYES [MZSP]; same locality, 02.VIII.1972, 1 worker, HALFFTER & REYES [MZSP]. Colima: Santiago,

14.I.1943, 2 workers, F. BONET [MZSP]. Guerrero: Acapulco, 06–07.X.1961, 1 worker, PEREIRA & HALFFTER [MZSP]; Revolcadero, XII.1963, 2 workers, 1 gyne, N. L. KRAUSS [USNM]. Yucatan: Chichenitza, VI.1929, 1 worker, 1 gyne, J. BEQUAERT [MCZC]. Campeche: 10 km E Campeche, 28–29.VII, 12.VIII.1953, 27 workers, 9 soldiers, E. O. WILSON [MCZC]. Quintana Roo: Cozumel, 08.VIII.1949, 1 worker, C. J. GOODNIGHT [MZSP]; same locality, VII.1959, 2 workers, N. L. H. KRAUSS [USNM]. Chiapas: Tapachula, V.1902, 2 workers, COOK & COLLINS [USNM]; same locality, V.1923, 2 workers, 3 soldiers, W. M. MANN [MHNG, MZSP]; Ocosingo Valley, 01–07.VII.1950, 1 gyne, GOODNIGHTS & STANNARD [MCZC].

Belize: Augustine, Pine Ridge, VII.1963, 2 workers, J. REISKIND [MCZC]; same locality, 03–07.VII.1963, 1 worker, C. C. PORTER [MCZC]; El Cayo, IX.1959, 6 workers, N. L. H. KRAUSS [USNM]; Cayo dist., Pine Mtn. Ridge, Rubber Camp, Macal River, 415 m, 21.II.1992, 1 worker, G. D. ALPERT [MCZC].

Guatemala: Chacoj, Vera Paz, 1 gyne, CHAMPION [MHNG]; Pantaleon, 3 gynes, CHAMPION [MHNG]; Escuintla, 27.XII.1911, 6 workers, 2 soldiers, W. M. WHEELER [MCZC, MZSP]; Patulul, 08.I.1912, 4 workers, 3 soldiers, W. M. WHEELER [MCZC]; Petén, July 1984, 3 workers [JSHC]; Zacapa, 13.XII.1911, 5 workers, 5 soldiers, W. M. WHEELER [MCZC]; Samarata, 3 workers, KELLERMAN [MCZC]; Livingston, 1 gyne, BARBER & SCHARZ [MCZC]; Bobas, V.1924, 6 workers, 4 soldiers, 5 gynes, 3 males, W. M. MANN [USNM].

El Salvador: San Salvador, X.1959, X.1965, 3 workers, N. H. L. KRAUSS [USNM]; same locality, 26.VI.1958, 1 worker, L. J. BOTTIMER [USNM]; same locality, 1 worker, 07.VI.1958, O. L. CARTWRIGHT [USNM]; Volcán de Conchagua, V.1958, 3 workers, L. J. BOTTIMER [USNM].

Honduras: no further locality, on Orchids, intercepted in Hoboken (New Jersey), 18.V.1941, 1 worker [MZSP]; no further locality, on *Tillandsia* sp. (leaf), intercepted in an U. S. Port of Entry, California, Los Angeles, 13.V.1982, 5 workers, 4 soldiers, 2 gynes, 8 males, [USNM]; La Ceiba, 23.IX.1911, 1 worker, F. J. DYER [MZSP]; same locality, 21.III.1920, 1 worker, W. M. MANN [USNM]; Amapalo, I.1933, 1 worker, A. H. STURTEVANT [USNM].

Nicaragua: Chinandega, 1 worker, BAKER [MCZC]; El Tuma, 30 km E Matagalpa, Highway 5, 330m, 19.VI.1978, 2 workers, KUGLER & HAHN [MCZC].

Costa Rica: no further locality, 1 worker, TOWSEND [MHNG]; no further locality, 1 gyne [MCSN]; no further locality, 1920, 1 worker, 1 gyne, P. SERRE [MNHN]; no further locality, 1 worker, SCHMIDT [MZSP]; no further locality, 5 workers, 1 soldier, F. NEVERMANN [MZSP]; La Caja, 1920, 1 gyne, P. SERRE [MNHN]; El Hiquito, San Mateo, 7 workers, BIOLLEY [MHNG, NHMB]; Salinas, 4 workers, ALFARO [MCSN]; Alajuela, 4 workers, 2 soldiers, March, 1896, A. ALFARO [MCSN]; same locality, Prov. Florencia, 11 mi N, 06.VII.1963, 4 workers, D. H. JANSEN [USNM]; Port Limón, 24–29.XI.1911, 10 workers, 11 soldiers, 2 gynes, W. M. WHEELER [MCZC, MZSP]; San José, 01.XII.1911, 9 workers, 11 soldiers, 1 male, W. M. WHEELER [MCZC]; same locality, 1940, 6 workers, 1 soldier, H. SCHMIDT [MZSP]; Santa Clara Pr., Hamburg Farm, 21–22.VIII.1925, 1 worker, 2 soldiers, F. NEVERMANN [MZSP]; same locality, from anteater's stomach, 1 worker, F. NEVERMANN [USNM]; Hamburg Farm, March, 5 workers, 1 soldier, C. P. DODGE [MZSP]; Ciruela, 22.IX.1929, 2 workers, A. ALFARO [MZSP]; Orotina, 07.XII.1929, 1 worker, 1 soldier, A. ALFARO [MZSP]; Liberia, 14–16.I & 01.IV.1930, 9 workers, 8 soldiers, A. ALFARO [MCZC, MZSP]; 5 km S of Liberia, Guanacaste Prov., 21.VIII.1963, 4 workers, 1 soldier, D. H. JANZEN [USNM]; Palmar, X.1959, 8 workers, 13 soldiers, E. O. WILSON [MCZC]; Punta Prov., Palmar Sur, 24.VIII.1965, 4 workers, 2 soldiers, F. COYLE [MZSP]; Tocumen, 26.IV.1961, 1 worker, N. L. KRAUSS [USNM]; Paraiso, 2.I & 06.IV.1911, 1 worker, E. A. SCHWARZ [USNM]; Curundu, 02.V.1972, 1 worker, R. & E. FROESCHNER [USNM]; Palo Verde, Field Stat., 28.I.1979, 4 workers, 4 soldiers, S. P. COVER [MCZC]; Summit, XI.1965, 1 worker, N. L. H. KRAUSS [USNM].

Panama: La Conception, 16.VII.1930, 1 worker, BIERIG [NHMB]; Juán Diaz, 11.VI.1930, 1 worker, BIERIG [NHMB]; Volcán Chiriqui, 1930, 1 worker, BIERIG [NHMB]; Bugaba, 2 workers, 3 soldiers, 1 gyne, CHAMPION [MHNG]; Monte Oscuro, 13.IV.1935, 2 workers [MCZC, MZSP]; Miraflores, 19.III.1923, 1 soldier, W. M. WHEELER [MCZC]; Ancon, 1 worker, A. H. JENNINGS [USNM]; Porto Bello, 11.III.1911, 1 worker, E. A. SCHWARTZ [USNM];

Patino, Pt. Darien, 31.VIII.1952, 1 worker, F. S. BLANTON [USNM]; Tumba Muerta, 5.IV.1923, 7 workers, 18 soldiers, 8 gynes, 3 males, in *Acacia spadicigera*, W. M. WHEELER [MCZC]; Barro Colorado Island, 8.VI & 23–24.VII.1924, 43 workers, 18 soldiers, 3 gynes, W. M. WHEELER [MCZC]; Barro Colorado, Nature Monument, Gigante Peninsula, 18.IV.1992, 4 workers, J. E. TOBIN [MCZC]; Río Agua Salud, 6.III.1923, 3 soldiers, 4 gynes, in *Acacia spadicigera*, W. M. WHEELER [MCZC]; Marajal nr. Colon, 11.VII.1924, 11 workers, 4 soldiers, in *Bixa orellana*, W. M. WHEELER [MCZC]; Corozal, 9.IV.1909, 1 worker, A. H. JENNINGS [USNM]; same locality, 21.XI.1911, 12.IX.1924, 4 workers, 9 soldiers, 4 gynes, W. M. WHEELER [MCZC]; Cuyuni River, 1 gyne, LAVARRE [MCZC]; Darien, Garachine, Feb.1953, 1 worker, F. S. BLANTON [USNM]; Ft. Amador, 18.VII.1924, 15 workers, 11 soldiers, 1 male, W. M. WHEELER [MCZC]; Ft. Sherman, 03.VII.1924, 2 workers, N. BANKS [MCZC]; Old Panama, 31.I.1911, 1 worker, E. A. SCHWARZ [USNM]; Frijoles, 10.VII.1924, 11 workers, 2 soldiers, W. M. WHEELER [MCZC]; Gamboa, 1924, 4 workers, 2 soldiers, N. BANKS [MCZC]; same locality, 01.V.1972, 1 worker, R. & E. FROESCHNER [USNM]; France Field, 02.VII.1924, 3 workers, 2 soldiers, D. E. WHEELER [MCZC].

Colombia: G u a j i r a : Puente Bomba, nr. Dibulla, 19.VI.1976, 4 workers, 2 soldiers, 2 gynes, 4 males, W. L. & D. E. BROWN [MCZC]; Serrania de Macuira, 6–8 km S of Nazareth, 80–100m, 70–200 m, 12–13.VI.1976, 6 workers, 4 soldiers, W. L. BROWN & R. C. KUGLER [MCZC]. M a g d a l e n a : San Pablo, 30. Juli, 1 worker [ZSMC]; Río Frío, March 1924, 2 workers, W. M. MANN [MZSP]; same locality, 3–7.III.1928, 1 worker, DARLINGTON [MCZC]; Aracataca, 3.V.1928, 1 worker, DARLINGTON [MCZC]. A n t i o q u i a : Medellin, I-II.1963, 1 worker, P. B. SCHNEBLE [MCZC]. C a l d a s : Chinchina, 15.VIII.1957, 3 workers [MCZC]. V a l l e : SW of Cali, above Barrio Siloé, 1000 m, 14 & 16.VII.1972, 19 workers, 3 soldiers, M. L. CORN [MZSP]. C a q u e t a : Venecia, VI.1936, 4 workers, R. ROBÁ [MCZC]. A m a z o n a s : Leticia, 70 m, 09.VIII.1973, 6 soldiers, M. L. CORN [MZSP].

Trinidad & Tobago: T r i n i d a d : no further locality, 1944, 3 workers, N. A. WEBER [MCZC]; Mayaro Bay, 4.XII.1934, 1 worker, N. A. WEBER [MCZC]; Salybia Bay, E Coast, 19.V.1935, 4 workers, 3 soldiers, N. A. WEBER [MCZC].

Venezuela: Anduze, 12.XI, 02.XII.1939, 3 workers [MCZC]. D e l t a A m a c u r o : Orinoco Delta, 31.I.1935, 16 workers, 6 gynes, N. A. WEBER [MCZC]. N u e v a E s p a r t a : I. Margarita, Pampatar, 27.II.1982, 1 worker, C. R. F. BRANDÃO et al. [MZSP]. D i s t r i t o F e d e r a l : Caracas, 1 soldier [MHNG]; same locality, 1 gyne, THIEME [MCSN]; El Valle, 07.VIII.1939, 1 gyne, G. VIVAS [MCZC]. Z u l i a : Carrasquero, 29–30.V & 15.VI.1976, 1 worker, A. S. MENE & D. VINCENT [USNM]. A n z o a t e g u i : 9 km S of Clarines, 02.XI.1986, 3 soldiers, E. M. CANCELLO et al. [MZSP]. M o n a g a s : Barrancas, R. Orinoco, Ja.-Feb.1935, 2 workers, 1 gyne, N. A. WEBER [MCZC]. B o l í v a r : Caicara, Riv. Orinoco, 1 worker, G. K. CHERRIE [USNM]; Ciudad Bolívar, 26.I.1935, 15 workers, N. A. WEBER [MCZC].

Guyana: E s s e q u i b o : no further locality; 2 workers (syntypes of *minutus*), SMIDT [ZMUC]; no further locality, 1 worker [MCSN]; Upper Essequibo, 01.XII.1935, 1 worker, I. G. MYERS [MCZC]; Mataruki, Upper Essequibo, 5.XII.1935, 1 worker, J. MYERS [MCZC]; S. Rupununi, Savannahs, 11.XI.1935, 1 worker, J. G. MYERS [MCZC]; Kartabo, Jul. -Aug. 1920, 49 workers, 44 soldiers, 21 gynes, W. M. WHEELER [MCZC, MZSP]; Bartica, 15–20.IX.1917, 3 workers, W. M. BEEBE & W. M. WHEELER [MCZC]; Fl. Settlement, R. Mazaruni, VIII.1935, 1 worker, N. A. WEBER [MCZC]. D e m e r a r a : Georgetown, 14.VII.1920, 1 worker, W. M. WHEELER [MCZC]; same locality, 9.VI.1936, 2 workers, N. A. WEBER [MCZC]; same locality, Botanic Gardens, 26.IX & 3.X.1918, 3 workers, H. MORRISON [USNM]; near Peter's Hall, 2 mi from Georgetown, 22.IX.1916, 9 workers, H. MORRISON [USNM]; River Bank, 1 & 2 mi from Georgetown, 22.IX.1918, 16 workers, H. MORRISON [USNM].

Surinam: no further locality, 1 gyne [MCSN]; v. Paramaribo, 14–17.V.1963, 1 worker, F. G. WERNER [MCZC].

French Guyana: Cayena, 2 workers, JELSKI [MHNG]; same locality, 2 workers, 1 soldier, MONTERO [MCSN]; Roches de Kourou, July, 1 gyne, LE MOULT [NHMB].

Brazil: no further locality, 1 worker (syntype of *volxemi*), C. VAN VOLXEM [MCSN]. A m a p á : Macapá, 5.V.1979, 1 worker, W. L. OVERAL [MPEG]; Curiaú, 19 & 23.XI.1981,

2 workers, GORAYEB et al. [MPEG]; Mazagão, 21.XI.1981, 1 worker [MPEG]; Pacoval, 14.XII.1982, 1 worker, M. F. TORRES [MPEG]; Highway BR. 156 km 14, border of Rio Matapi, 31.XI.1981, 2 workers [MPEG]. A m a z o n a s : no further locality, 9 workers, 5 soldiers, H. W. BATES [MHNG, ZSMC]; Tefé, no further data, 1 gyne (holotype of *cognatus*) [BMNH]; Amazon River, 1855, 1 worker, STEVENS [NHMB]; Presidente Figueiredo, BR–174, km 157, 14.IV.1990, 4 workers, A. Y. HARADA [INPA]; BR–174, km 44, 25.II.1983, 1 worker, A. Y. HARADA [INPA]; Ponta Negra N of Manaus, 1.IX.1962, 7 workers, 3 soldiers, W. L. BROWN [MCZC]; Manaus, INPA, V–8, 26.VIII.1982, A. Y. HARADA [INPA]; same locality, 3 workers, MANN & BAKER [MCZC]; same locality, IX.1962, 14 workers, 1 soldier, K. LENKO [MZSP]; Tarumã-Mirim, 12.I.1976, 1 worker, J. ADIS [INPA]; Reserva Florestal A. Ducke, 2°55' S, 59°59' W, 27.X.1982, 1 worker, ADIS et al. [INPA]; same locality, 22–26.I.1996, 42 workers, 5 soldiers, M. L. DE ANDRADE [INPA]; Igar. Tarumãnzinho N of Manaus, 30.X.1987, 1 worker, C. R. F. BRANDÃO & J. M. DINIZ [MZSP]; nr. Anavilhana, left side of R. Negro, 21.IV.1967, 1 worker, Exp. Dep. Zool. [MZSP]; Rio Tatobi, III.1976, 1 worker, A. S. SHELLEY [MZSP]. P a r á : Belém-Tapanã, 8.XII.1982, 3 workers, A. Y. HARADA [INPA; MZSP]; Tocantins Itaguatins, Ilha S. Domingos, 17–19.VII.1989, 4 workers, F. F. RAMOS [MPEG]; Serra Norte, Fofoca, 17.IV.1983, 1 worker, F. F. RAMOS [MPEG]; Serra Norte, 3 Alpha, 26.VI.1985, 1 worker, M. ZANUTO [MPEG]; Serra Norte, Manganês, 10.VI.1983, 1 worker, FRANÇA [MPEG]; Serra Norte, C. Rupestre, 2–9.IX.1983, 3 workers, R. B. NETO & M. F. TORRES [MPEG]; Ponta de Pedras, 5.III.1979, 1 worker, M. F. TORRES [MPEG]; Tucuruí, left side, 12–13.III.1979, 2 workers, R. B. NETO & W. L. OVERAL [MPEG]; São João de Pirabas, 20–22.XII.1992, 1 worker, J. DIAS [MPEG]; Bragança, 12.III.1983, 1 worker, R. B. NETO [MPEG]; Conceição do Araguaia, 17–21.XI.1979, 1 soldier, W. L. OVERAL [MPEG]; Alenquer, 5.VII.1979, 1 worker, W. FRANÇA [MPEG]; Primavera, Boa Vista, Ilha Arapiranga, 23–24.XI.1992, 2 workers, J. DIAS [MPEG]; Algodoal, 9–11.I.1991, 4 workers, A. Y. HARADA [INPA]; Belém, 06–19 & 22.IV.1963, 2 workers, WERNER [MCZC]; same locality, APEG, 24.X.1969, 14 workers, 6 soldiers, N. ROSA [MZSP]; Santarém, Taperinha, 2°54' S, 54°20' W, 14.X.1980, 4 workers, R. L. JEANNE [MCZC]; Caldeirão, Rio Itacaiunas, VII-VIII.1985, 1 worker, C. R. F. BRANDÃO & W. BENSON [MZSP]; S. Norte, Carajás, Mata Manganês, 30.VII-VIII.1985, 1 worker, C. R. F. BRANDÃO & W. BENSON [MZSP]; Carajás, VII-VIII.1985, 2 workers, C. R. F. BRANDÃO & W. BENSON [MZSP]; Oriximiná, Alcor e Alta, 12.X.1982, 2 workers, A. Y. HARADA [MZSP]; Jacareacanga, XII.1968, 1 worker, M. ALVARENGA [MZSP]; Alto Parú, IX.1928, 1 worker, SAMPAIO [MZSP]; Cachoeira do Breu, X.1928, 1 worker, SAMPAIO [MZSP]; Óbidos, II.1949, 1 worker [MZSP]; Conceição do Araguaia, 01–02.II.1983, 1 worker, J. A. RAFAEL [MZSP]. M a r a n h ã o : Imperatriz, Rbeirãozinho, 2–5.VIII.1989, 1 worker, F. F. RAMOS [MPEG]. P i a u í : Estação Ecológica Uruçuí-Una, Ribeiro Gonçalves, 7.XII.1982, 2 workers, A. J. ALMEIDA [MZSP]; Terezinha, 2 workers [MPEG]; 20 km S of Floriano, Buriti Sol, 05–12.XI.1991, 1 worker, BRANDÃO & MOUTINHO [MZSP]; 5 km E of Oeiras, Fazenda Talhada, 13–17.XI.1991, 1 worker, BRANDÃO & MOUTINHO [MZSP]; Canto do Buriti, 18–22.XI.1991, 1 worker, C. R. F. BRANDÃO [MZSP]; 10 km N of Corrente, Fazenda Maracujá, 23–27.XI.1991, 1 soldier, C. R. F. BRANDÃO [MZSP]. C e a r á : no further locality, 4 workers, 1 soldier, ROCHA [MHNG]; Porto Trombetas, VIII.1992, 4 workers, J. D. MAYER [MZSP]. R i o G r a n d e d o N o r t e : Natal, 4 workers, 1 soldier, 1 gyne, W. M. MANN [MCZC, MZSP, USNM]; same locality, 1953, 1 worker, 2 soldiers, P. MELO [MZSP]; Ceará-Mirim, 1 gyne, W. M. MANN [MCZC]. A l a g o a s : Coruripe, 2.X.1979, 2 workers, F. M. Oliveira [MPEG]; Maceió, 02–06.II.1976, 6 workers, 1 gyne, F. LANE [MZSP]. P e r n a m b u c o : Caruaru, IV.1972, 2 workers, M. ALVARENGA [MZSP]; same locality, 2 workers, 1 soldier, 1 gyne, 2 males, PICKEL [MZSP]; Tapera, 1 worker, PICKEL [MZSP]; Serra dos Prazeres, nr. Recife, 9.VII.1944, 1 worker, R. L. WENZEL [MZSP]; Recife, 1938, 2 workers, 2 soldiers, L. LIMA CASTRO [MZSP]. A c r e : Cruzeiro do Sul, 70.VI, 14.VII.1973, 1 worker, R. H. PIRES [MZSP]; Porto Valter, X.1961, 1 worker, P. L. HERBST [MZSP]; Rio Branco, 01.IV.1954, 2 workers, M. ALVARENGA [MZSP]; same locality, Parque Zoobotânico Cidade Universitária 28.XI.1987, 2 workers, E. DEUS [MZSP]. R o n d ô n i a : Vilhena, 25.VII.1983, 1 worker, A. Y. HARADA [INPA]; same locality, XI.1973, 4 workers, M. ALVARENGA [MZSP].

Goiás: Jataí, XII.1972, 3 workers, 2 gynes, F. M. OLIVEIRA [MZSP]; Jataí, Fazenda Aceiro, 2.XI.1962, 42 workers, 10 soldiers, 7 gynes, 3 males, Exp. Dep. Zool. [MCZC]; same locality, Fazenda Cachoerinha, 29.XI.1962, 4 workers, 1 soldier, 2 gynes, Exp. Dep. Zool. [MZSP]; Anápolis, 12.II.1958, 1.I.1966, 10 workers, W. W. KEMPF [MZSP]; 7 km NW Alto Paraíso, Morro das Cobras, 1–7.VII.1991, 1 worker, C. R. F. BRANDÃO et al. [MZSP]. Bahia: no further locality, 2 workers, 1 gyne, BONDAR [NHMB]; Encruzilhada, 960 m, XI.1972, 3 workers, SEABRA & ALVARENGA [MZSP]; Maracás, Fazenda Maria Inácia, 24–29.XI.1990, 1 worker, C. R. F. BRANDÃO & J. M. DINIZ [MZSP]; Ilhéus, 10.IV.1991 & 5.I.1994, 2 workers, 1 soldier, 1 gyne, J. H. C. DELABIE [CPCC]. Distrito Federal: Brasilia, 7.V.1979, 1 worker, R. B. NETO [MPEG]. Mato Grosso: no further locality, 2 gynes [MCSN, MHNG]; Rondonópolis, Area Indíg. Tadarinana, 16°28' S, 54°38' W, 31.X.1991, 1 worker, MOERICKE [MZSP]; Mato Verde, 15.III.1941, 1 gyne, R. LUZ [MZSP]; Sinop, 55°37' W, 12°31' S, X.1974 & X.1976, 6 workers, 2 soldiers, M. ALVARENGA [MZSP, MPEG]. Mato Grosso do Sul: Utiariti, Rio Papagaio, 325 m, VII-VIII. 1961, 40 workers, 25 soldiers, 3 gynes, LENKO [MZSP]; same locality, 27–30.X, 2.XI.1966, 30 workers, 8 soldiers, 12 gynes, LENKO & PEREIRA [MZSP]; Itaum, III.1974, 1 soldier, M. ALVARENGA [MZSP]; Três Lagoas, Fazenda Canaã, 08–14.I.1972, 3 workers, F. LANE [MZSP]; same locality, Fazenda Dr. José Mendes, 14–24.X.1964, 5 workers, Exp. Dep. Zool. [MZSP]; Limoeiro, 10 km S of Ilha Taiamã, 8.VIII.1980, 1 worker, C. R. F. BRANDÃO [MZSP]; Jardim, I.1962, 3 workers, R. MUELLER [MZSP]; Imbirussú-Corumbá, 01.XII.1960, 2 workers, 2 soldiers, 1 gyne, K. LENKO [MZSP]; Serra do Urucum, Corumbá, 25.XI.1960, 14 workers, 3 soldiers, 4 gynes, 2 males, K. LENKO [MZSP]. Minas Gerais: Dourados, Colonia Vicentina, I.1962, 3 workers, MUELLER [MZSP]; Lagoa Formosa, Cabeceiras, 24–25.X.1954, 1 worker, Exp. Dep. Zool. [MZSP]; Pedra Azul, 800 m, XI.1972, 3 workers, 1 gyne, SEABRA & ALVARENGA [MZSP]; Matosinhos, July 1926, 1 worker, PARTBERG [MZSP]. Espírito Santo: Linhares, IX.1972, 2 workers, M. ALVARENGA [MZSP]. Rio de Janeiro: no further locality, 1 worker [MHNG]; no further locality, 1 worker, SAMPAIO [MHNG]; Copacabana, 1 worker, GÖLDI [MHNG]; Repr. Rio Grande, 15.III.1961, 06.IV.1962, VI.1972, 14 workers, 3 soldiers, 3 gynes, 1 male, F. M. OLIVEIRA [MZSP]; Fl. da Tijuca, IV.1966, 1 soldier, M. ALVARENGA [MZSP]; Marambaia, I.1960, 1 worker, R. MUELLER [MZSP]. São Paulo: Santos, 28.IX.1891, 2 gynes [ZSMC]; Agudos, 08.XI.1952, 07-13.IX.1953, 11 workers, 1 soldier, 7gynes, 1 male, W. W. KEMPF [MCZC]; same locality, 01.VI, 29.VIII.1958, 17 workers, 1 soldier, R. MUELLER [MZSP]; Silva Jardim, III.1974, 2 workers, 1 soldier, W. W. KEMPF [MZSP]; Boa Esperança do Sul, Fazenda Itaquerê, 26.I.1964, 2 workers, 3 soldiers, K. LENKO [MZSP]; Orlândia, V.1060, 1 worker, R. MUELLER [MZSP]; Araraquara, 24.III.1990, 1 worker, M. L. DE ANDRADE [NHMB]; Assis, 31.I.1974, 1 worker, W. W. KEMPF [MZSP]; Teodoro Sampaio, XI.1973, 2 workers, F. M. OLIVEIRA [MZSP]; Itanhaem, 10.XI.1961, 6 workers, W. W. KEMPF [MZSP]; Cajuru, 7.VIII, 13.X, 31.XII.1992, 22.2.1993, 17 workers, A. SILVESTRI [MZSP]. Paraná: Registro, 17.V.1964, 2 workers, F. LANE [MZSP]; Bocaiuva, XII.1963, 1 gyne, F. PLAUMANN [MZSP]; Rolândia, III.1975, 1 worker, M. ALVARENGA [MZSP]; Foz do Iguaçu, VII.1961, 1 worker, N. L. H. KRAUSS [USNM].

Peru: Madre de Dios: Río Tombopata, Res. 30 km SW Pto. Maldonado, 12°50' S, 069°20' W, 01.III.1982, 2 workers, T. L. ERWIN et al. [MCZC].

Bolivia: Beni: Rurrenabaque, Oct. 1921, 4 workers, 1 soldier, 4 gynes, 2 males, W. M. MANN [MZSP]; Riberalta, I.1922, 2 workers, 1 soldier, W. M. MANN [MZSP]; Reyes, Oct. 1921, 5 workers, 1 gyne, W. M. MANN [MZSP, USNM]; Huachi, VIII.1921, 1 gyne, W. M. MANN [USNM]. La Paz: Coroico-Chilumani, 1891, 1600 m, 1 worker, BALZAN [MCSN]; Covendo, 1921–1922, 5 workers, 5 soldiers, W. M. MANN [MZSP].

Argentina: Misiones: Ignacio, V.1961, 1 worker, KRAUSS [USNM].

Paraguay: no further locality, 1 worker, BALZAN [MCSN]. La Cordillera: S. Bernardino, 4 workers, 6 soldiers, 2 gynes, K. FIEBRIG [MHNG, ZSMC]; Asunción, VII. 1961, 1 worker, N. L. H. KRAUSS [USNM]. Alto Paraná: Pastoreo, I.1927, 1 gyne, D. WEES [MCZC].

D i s c u s s i o n . - *Minutus* is the sister species of *simillimus* with which it is very similar and partially sympatric. It is also one of the commonest species of the genus and the one with the broadest geographical distribution in absolute. The synonymy of *cognatus* (described on one gyne only) with *minutus* leaves no doubt after comparison of the *cognatus* holotype with the worker-associated gynes of *minutus* available for the present study. The heads of soldiers and gynes from the northern range of the species are more flat than those from other areas. An important location of variation which appears to be not geographically correlated is the declivous face of the propodeum: it can be either longitudinally or transversely striate according to the specimens.

FERNÁNDEZ et al. (1996) report this species also from the Colombian states of Cundinamarca, Huila, and Meta.

D i s t r i b u t i o n : Mexico, St. Thomas Island, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Guyanas, Brazil, Peru, Bolivia, Argentina, Paraguay.

Cephalotes simillimus (KEMPF) new combination and new status

Figs. 84, 387 (bottom)

Cryptocerus minutus var. *cognatus* (sic) SMITH, SANTSCHI, 1931 a: 275. Partim. Soldier. Nec worker (= *pusillus*). Misidentification.

Paracryptocerus simillimus KEMPF, 1951: 184, figs. 125, 126. Worker, soldier. Original description. Type locality: Kartabo (Guyana). Type material: holotype worker in MCZC, 13 syntype workers, 6 syntype soldiers labelled: "Kartabo. B. G., Jul. Aug. 1920, W. M. Wheeler Collection", MCZC and MZSP, examined.

Zacryptocerus simillimus (KEMPF), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *laminatus* clade characterised in the worker by the eyes broader than 1/3 of the head length, in the worker and in the soldier by the propodeal spines expanded ventrally into a lamella.

W o r k e r (Figs. 84, 387 bottom) (description of KEMPF, 1951). - "Length 3.9 mm. Median head length 1.00 mm; Weber's length of thorax 1.12 mm. Black; the following ferruginous: apex of mandibles, antennae, tip of femora, tibiae, tarsi, apical gastral segments, epinotal and petiolar spines. Frontal carinae yellowish-brown.

Head opaque, longer than broad, broadest behind the eyes; interocular distance distinctly shorter than maximum length of head (45 : 50). Lateral margins somewhat sinuate above the eyes, posterior margin straight mesad; the occipital angles with slightly projecting subtransversely truncate entirely infuscated lamellae, the apical border of which is nearly straight. Cheeks strongly marginate beneath, densely covered with silvery, appressed, scale-like hairs. Eyes large, their longest diameter more than 1/3 of median head length. Upper and lower surface of head finely reticulate-punctate, sparsely covered with slender, flattened, simple, appressed, silvery scale-like hairs; slightly larger, denser and somewhat canaliculate, in grooves, in front of the occipital border.

Thorax subopaque. Anterior border moderately arcuate, shoulders acutely angulate. Pronotum somewhat expanded behind laterally with small triangular teeth on each side, coalesced at their base, the posterior being smaller than the anterior tooth. Posterior corners of pronotum in the form of a subrectangular tooth, projecting. Promesonotal suture vestigial. Mesonotum comparatively broader and shorter than in *minutus*, each side with a small, acute tooth. Mesoepinotal suture distinct and impressed. Basal face of epinotum in the same plane as mesonotum, transverse, with two broad, flat, triangular teeth on each side, the posterior being somewhat longer. The posterior border of the second tooth forms a sharp crest which delimits the declivity laterad and behind. Dorsum of thorax flat, scarcely convex. Declivous

face excavated mesad, not striated longitudinally. The entire thorax finely reticulate-punctate, dorsum with dense, elongated grooves, harboring more or less canaliculate, silvery appressed scales, denser than on head. Declivity without scales below. Laterotergites of pronotum and mesopleura indistinctly longitudinally rugose, not striated.

Petiole opaque, transverse, with distinctly set off, slender, long, lateral spine, arising from the anterior corner, pointing slightly backwards. Postpetiole as long as petiole, transverse, with shorter, broader, apically subtruncate lateral spines, curving obliquely forward. Both peduncular segments finely reticulate-punctate with scattered glistening scales.

Gaster subopaque, subcordiform, depressed, moderately convex above. First gastral tergite emarginate antero-mesally, sharply crested antero-laterad, not forming a distinct set off lamellate border. Tergites and sternites finely reticulate-punctate. Scale-like silvery hair appressed, simple, rather dense. Erect pile confined to 2d –4th tergites and the sternites."

Measurements (in mm) and indices: TL 3.66–4.18; HL 0.91–1.00; HW 1.08–1.22; EL 0.32–0.37; PW 0.83–0.92; PeW 0.50–0.58; PpW 0.43–0.49; HBaL 0.36–0.40; HBaW 0.07–0.08; CI 116.4–125.0; PI 125.0–130.4; PPeI 156.4–169.2; PPpI 186.9–197.9; HBaI 18.9–20.5.

S o l d i e r (description of KEMPF, 1951). - "Length 5.9 mm. Median head length 1.65 mm; Weber's length of thorax 1.73 mm. Black; the following ferruginous: outer border of frontal carinae, antennae, tibiae, tarsi, tips of femora, apical border of gastral tergites and sternites.

Head subfulgid, scarcely longer than wide. Frontal carinae arcuate, diverging caudad to above the posterior end of the antennal scrobe, where they form a distinct yet very obtuse angle, prolonged above the eyes, but more or less obsolete, never forming a raised crest. Occiput distinctly truncate, the upper border not sharply marginate above. Occipital corners rounded. Occipital border blunt, slightly convex. Upper surface of head moderately convex above, slightly impressed mesad, cheeks immarginate below. Upper surface of head very finely punctate, with sparse, small foveolae, in which no distinct hair is visible. Foveolae slightly larger on occiput, still larger containing a visible, decumbent seta, on lower surface of head.

Thorax subfulgid above. Anterior border arcuate, shoulders rounded, sides of pronotum diverging posteriorly with a short, stout and acute, lateral tooth, pointing obliquely forward, then parallel and straight until reaching the lateral corner of the bluntly rounded more or less vestigial and mesally interrupted transverse pronotal keel, then converging towards the mesonotum. Posterior corners rounded. Promesonotum in profile greatly convex. Promesonotal suture vestigial. Mesonotum with a stout and bluntly rounded lateral tooth. Mesoepinotal suture impressed and distinct. Epinotum subopaque. Basal face of epinotum transverse, the posterior border concave and submarginate. Sides with an anterolateral broad, short, triangular tooth and a somewhat longer and more acute, posterior spine which is greatly diverging, having beneath a crest which delimits the entire side of the declivous face, and with a small tooth projecting from the crest beneath the posterior epinotal spine. Declivous face without macrosculpture. Microsculpture of promesonotum as on head, epinotum and sides of thorax finely reticulate-punctate. Upper surface of thorax with sparse, deeply impressed foveolae, rounded on promesonotum, elongate and not as deep on epinotum. Sides of thorax without macrosculpture; declivous face with transversely arcuate, more or less vestigial rugosities.

Petiole opaque, transverse, with a short, stout, subacute and recurved lateral tooth. Posterior half shallowly transversely concave. Postpetiole slightly longer than petiole, as wide as petiole, with very broad, plate-like, apically truncate, lateral projections.

Gaster subopaque, elongate; anterior border deeply emarginate; anterolaterally strongly marginate, without forming a distinct lamellate border. Sides of gaster moderately convex. Tergites and sternites finely reticulate-punctate, without foveolae.

All foveolae, except the ones on the upper surface of head and promesonotum have a distinct, decumbent, flattened seta, which is shiny and scale-like on the epinotum. Sides sparsely scaled. Gaster with small, decumbent, shiny scales. Erect pile confined to the tergites 2 – 4, the sternites and the posterior half of the first tergite of the gaster."

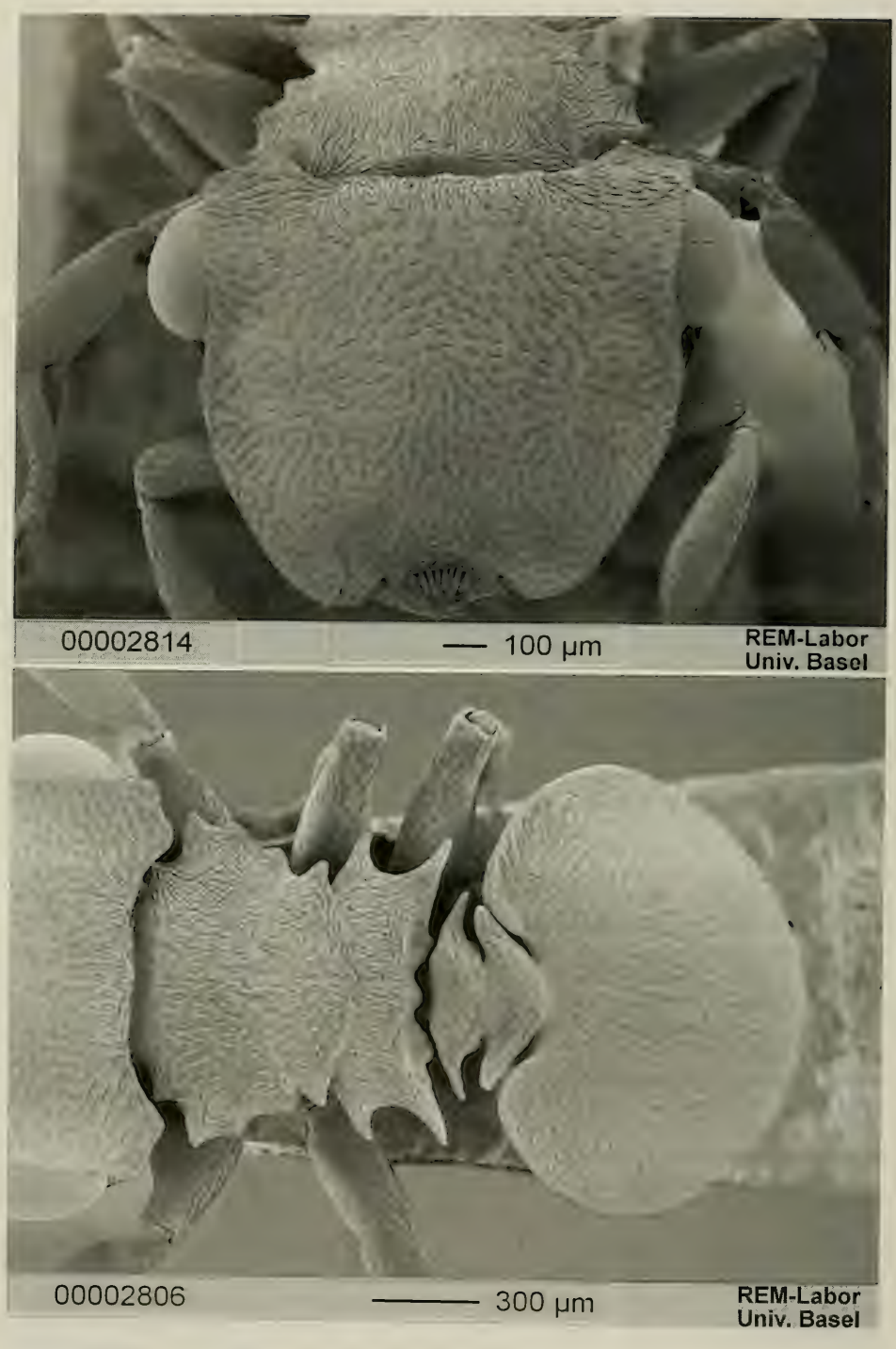


Fig. 84. *Cephalotes simillimus* (Kempf). Worker from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 4.98–6.48; HL 1.40–1.68; HW 1.52–1.76; EL 0.40–0.45; PW 1.24–1.54; PeW 0.63–0.77; PpW 0.62–0.72; HBaL 0.42–0.44; HBaW 0.11–0.12; CI 104.8–108.6; PI 114.3–122.6; PPeI 189.2–205.8; PPpI 194..4–213.9; HBaI 25.6–28.6.

Material examined. - **Guyana**: Essequibo: Kartabo, Jul. -Aug. 1920, 14 workers (holotype and paratypes), 6 soldiers (paratypes), W. M. Wheeler [MCZC, MZSP]; same locality and collector, 16 workers, 1 soldier (probably also belonging to the *simillimus* type series) [MCZC]; Kassikaityu R. 19.XI.1935, 1 worker, J. G. Myers [MCZC]; Upper Essequibo, 01.XII.1935, 1 worker, J. G. Myers [MCZC]; Essequibo River, Moraballi Creek, 1929, 1 soldier, Oxford Univ. Exp. [MCZC].

French Guyana: no further locality, 1 soldier (stratotype of *minutus* v. *cognatus*) [NHMB].

Brazil: Roraima: Rio Uraricoera, Ilha de Maracá, 18–28.VIII.1987, 1 worker, J. A. Rafael [INPA]. Amazonas: Res. Fl. A. Ducke, 26 km NE Manaus, 28.II.1978, 1 worker, J. Arias & N. Penny [INPA]; same locality, 16.X.1981, 2 workers, J. A. Rafael [INPA]; same locality, 21.VIII.1992, 1 worker, J. Adis et al. [INPA]; same locality, 16.III, 28.V, 30.VI, 12 & 29.XI, 26.VIII.1982, 23.II.1992, 12 workers, Adis et al. [INPA]; same locality, 28.IX.1981, 1 worker, J. A. Rafael [INPA]; same locality, 22–26.I.1996, 1 worker, M. L. de Andrade [INPA]; Manaus, V.1982, 2 workers [INPA]; Manaus, Estr. Am. km 1, 07.V.1971, 1 worker [MZSP]; Maraã, Rio Japurá, 11–17.X.1988, 1 worker, J. Dias [MPEG]. Pará: no further locality, 1 worker [MCSN]; Vigia, Campina, Ilha de Mata, 7.XII.1988, 2 workers, W. França [MPEG]; Belém, 20.I.1976, 1 worker, V. P. Daniel [MZSP]. Acre: Porto Acre, Humaitá, 15.VI–2.VII.1992, 1 worker, Gorayeb [MPEG]; Rio Branco, 25.X–8.XI.1991, 1 worker, F. Ramos et al. [MPEG]. Rondônia: Porto Velho, 29.X.1953, 2 workers, C. R. Gonçalves [MZSP]; Porto Velho, Rio Madeira, 2 workers, Mann & Baker [MCZC]. Bahia: Una, UNACAU, 09.V.1991, 2 workers, 1 soldier, Bernardos [CPCC]. Mato Grosso: Sinop, 55°37' W, 12°31' S, X.1974, 3 workers, M. Alvarenga [MZSP].

Peru: Madre de Dios: Río Tambopata Res., 290 m, 12°50' S, 69°20' W, 01 & 09.III.1982, 5 workers, 1 soldier, T. L. Erwin [MCZC].

Discussion. - Kempf (1951) described this species in part on Bolivian specimens too. We did not see any Bolivian example. Some workers from Amazonas and from Guyana have reduced propodeal lamellae, converging in this way with *minutus*. On the basis of the material available for the present study, however, we have no reasons to doubt the specific status of *simillimus*. The same apparently *minutus*-convergent workers contrast with other examples of *simillimus* also for having a reduced pilosity, a character we encountered also in an additional Amazonian worker with otherwise regularly lamellate propodeum.

Fernández et al. (1996) report this species from the Colombian states of Amazonas and Caquetá.

Distribution: Colombia, Guyanas, Brazil, Peru, Bolivia.

Cephalotes christopherseni (Forel) new combination

Figs. 85, 86, 87, 88, 89

Cryptocerus laminatus christopherseni Forel, 1912: 204. Worker and soldier. Original description. Type locality: Several localities in Colombia, Panama without further locality. Type material: lectotype and one paralectotype workers labelled: "Santa Marta, Colombie" selected by Kempf (1951) in MHNG, examined, 7 workers same label as the lectotype, 7 syntype workers labelled "Dibulla, Colombie", two syntype workers and 1 soldier labelled "Panama, Christophersen", all in MHNG, examined; one worker labelled "Dibulla, Colombie" in NHMB examined.

Paracryptocerus laminatus christopherseni (Forel), Kempf, 1951: 166, figs. 119, 120. First combination in *Paracryptocerus*.

Paracryptocerus christopherseni (FOREL), KEMPF, 1972: 176.
Zacryptocerus christopherseni, WHEELER, 1984: 173. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *laminatus* clade differing from other species of the clade by the autapomorphic loss of the gastral spots of the gyne, substituted by a dark reddish macula. Among the closest related species, *christopherseni* workers can be separated from those of *spinosus* by the shorter vertexal lamellae, and, in the worker and in the soldier, by the shorter gastral lamellae, by the presence of mesonotal spines and by the absence of golden hairs on the mesosoma. From *minutus* and *simillimus* this species differs for having a bispinose (not lamellate) pronotum.

W o r k e r (Fig. 85) (description of KEMPF, 1951). - "Length 5.4 mm. Median head length 1.36 mm. Weber's length of thorax 1.57 mm. Black; the following light ferruginous: frontal carinae, occipital lamellae, tip of last funicular segment, lamellate border of first gastral tergite. The following slightly darker: 1st funicular segment, apices of thoracic spines, peduncular teeth, apices of tarsal segments.

Head subopaque; slightly broader than long, broadest behind the eyes, narrowed in front, interocular distance slightly longer than maximum length of head (71:69). Posterior margin straight, the occipital angles with projecting obliquely truncate lamellae, the apical border of which is scarcely sinuate. Cheeks strongly marginate beneath, densely scaled. Eyes small, their maximum diameter distinctly less than one third of the median head length. Integument very finely reticulate-punctate, sparsely covered with silvery, slender, simple, appressed scale-like hairs, longer than in *inaequalis*, larger, canaliculate, situated in grooves in front of the occipital border.

Thorax opaque. Anterior border moderately arcuate, shoulders sharply angulate. Pronotum somewhat expanded laterally behind the shoulders, with two short, unequal and slightly upturned spines on each side, the posterior spine being shorter than the anterior. Posterior corner of pronotum projecting, as a more or less rectangular tooth. Promesonotal suture vestigial. Mesonotum with a small and acute lateral tooth. Mesoepinotal suture more or less distinct. Basal face of epinotum in the same plane as mesonotum, transverse, with a short and straight anterolateral spine, as long as the second pronotal spine and a much longer, slender spine projecting laterad and somewhat caudad from the posterior corner. Microsculpture as on head, but the very sparse, mostly canaliculate, decumbent, silvery, long scales lie in elongate grooves. Declivous face of epinotum not excavated mesally nor crested laterad. Laterotergite of pronotum and mesopleura longitudinally striated.

Petiole opaque, transverse, with distinctly set off, slender, long, subacute lateral spines, arising from the anterior corner. Postpetiole slightly longer than petiole, transverse, with shorter, broader, apically rounded, lateral spine, curving slightly forward. Both segments sculptured as thorax, the scales somewhat shorter and simple, not lying in distinct grooves.

Gaster subfulgid, elongate cordiform, very convex above. First gastral tergite with rather narrow, distinctly set off anterolateral lamellate border. Tergites and sternites finely and rather sharply reticulate-punctate. Scales of gaster sparser, simple, short, not lying in foveolae. Erect pilosity confined to 2nd to 4th tergites and sternites."

Measurements (in mm) and indices: TL 4.48–5.56; HL 1.10–1.32; HW 1.48–1.84; EL 0.34–0.40; PW 1.20–1.52; PeW 0.56–0.60; PpW 0.52–0.60; HBaL 0.52–0.60; HBaW 0.11–0.14; CI 134.5–139.4; PI 121.0–133.3; PPeI 200.0–271.4; PPpI 213.3–253.3; HBaI 21.1–23.3.

S o l d i e r (Fig. 86) (description of KEMPF, 1951). - "Length 7.0 mm. Median head length 1.83 mm; Weber's length of thorax 2.00. Black; the following ferruginous: frontal carinae in part (partly translucid), tip of last antennal segment, outer face of tibiae, tip of femora, three apical segments of tarsi. Fuscous: remaining part of appendages. Lamellate border of first gastral tergite semitranslucid.

Head subopaque; shorter than wide in front of the eyes (86:93). Frontal carinae greatly rounded anteriorly, prolonged and slightly upturned above the eyes in the form of a raised carinule, fading out before reaching the subangulate and projecting occipital corner. Upper

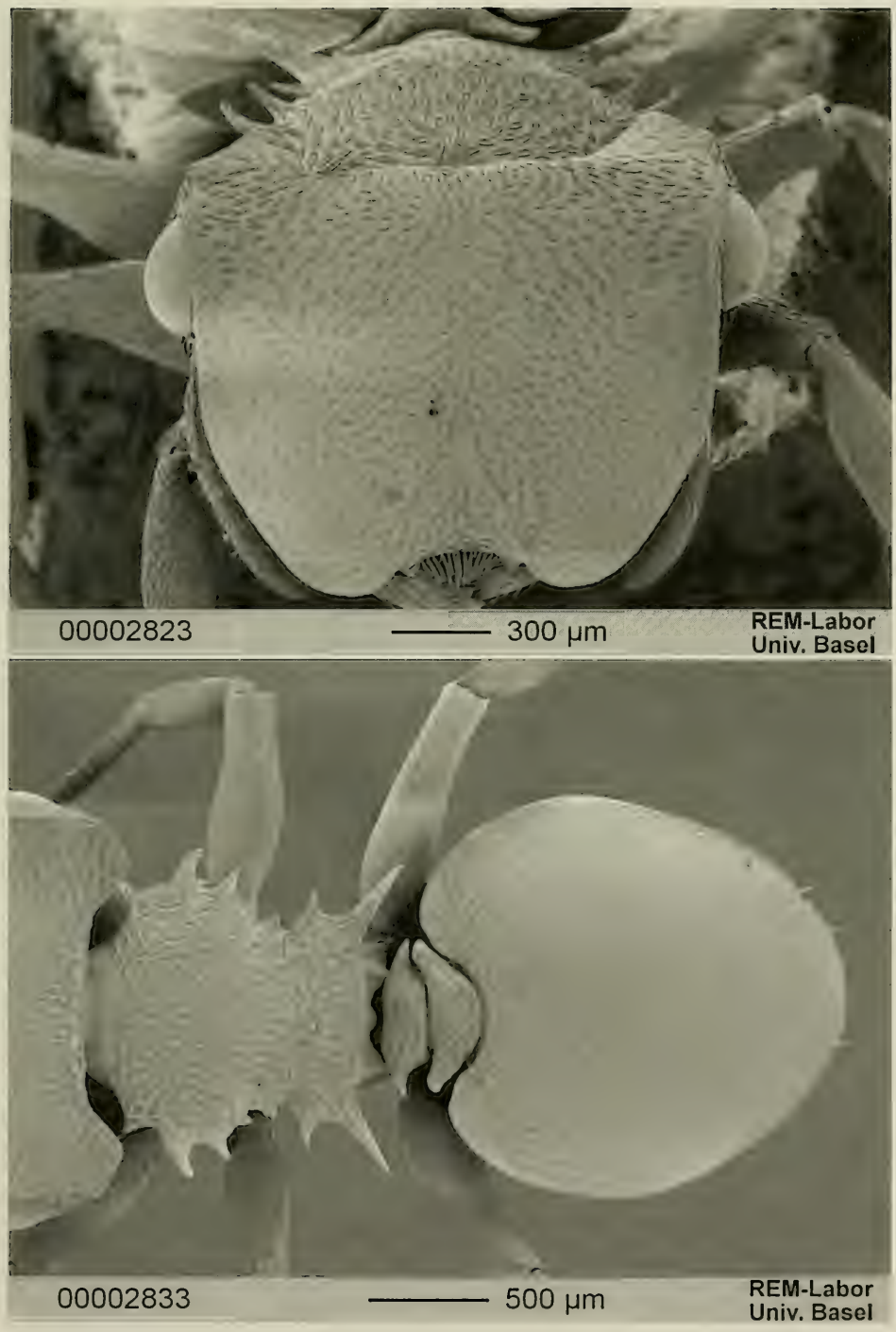


Fig. 85. *Cephalotes christopherseni* (FOREL). Worker from Barro Colorado Is., Panama: head (top) and meso- and metasoma (bottom) in dorsal view.

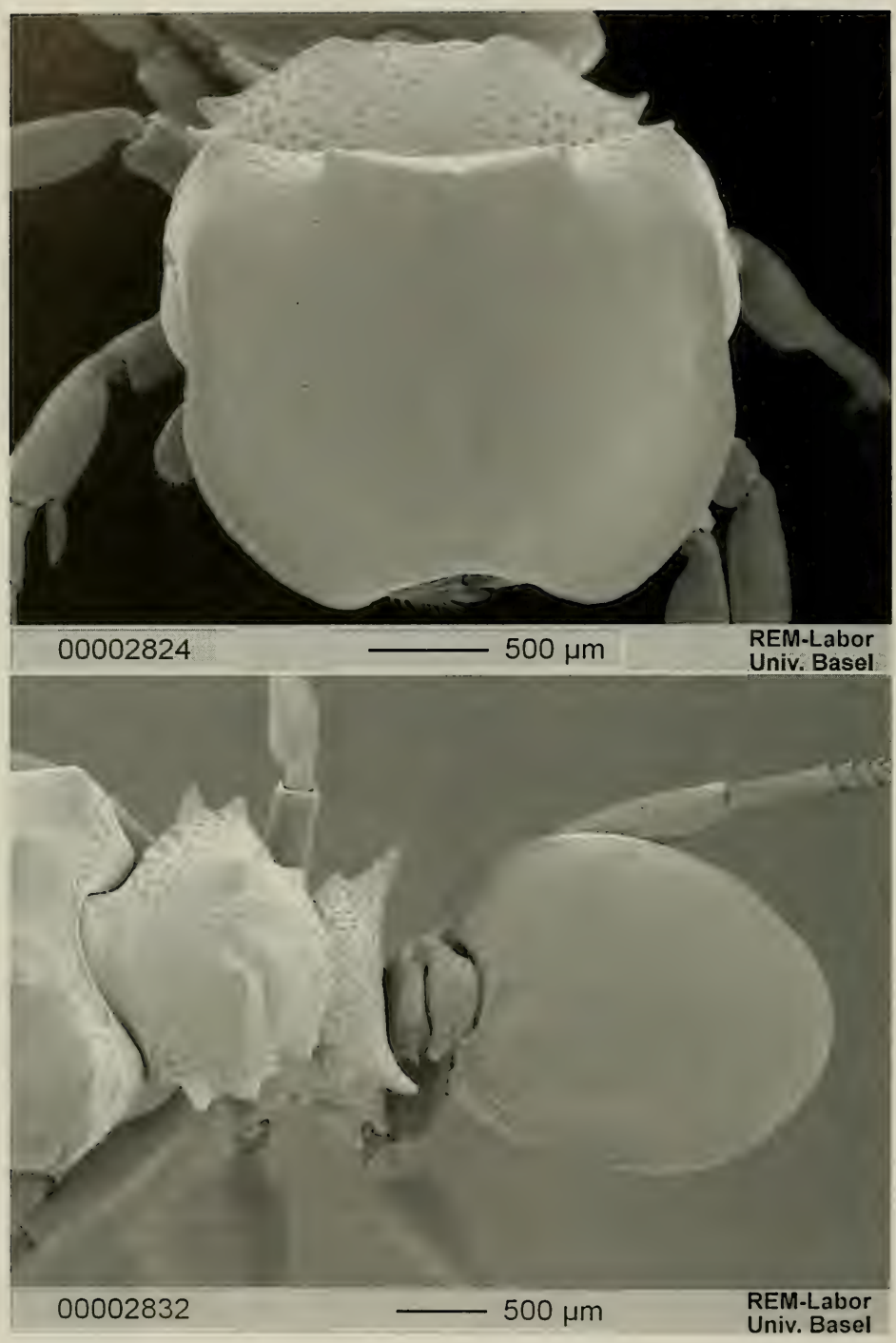


Fig. 86. *Cephalotes christopherseni* (FOREL). Soldier from Barro Colorado Is., Panama: head (top) and meso- and metasoma (bottom) in dorsal view.

surface of head very little convex. Eyes scarcely convex. Vertex with a pair of dentiform projections, occipital border between these teeth distinctly and sharply marginate. Occiput truncate mesad. Cheeks immarginate beneath. A distinct carinule below the eyes, extending to the occipital corners. Integument finely and shallowly reticulate-punctate. Upper surface of head with sparse, small foveolae, containing no distinctly visible hair. Foveolae somewhat more crowded on occiput. Sparser but larger on lower surface of head, containing a distinctly visible decumbent seta.

Thorax subopaque above. Anterior border arcuate, shoulders subangulate, not visible from above. Pronotum expanded laterally with two small, rather blunt teeth on each side; between the posterior pair of teeth a transverse crest, broadly interrupted mesad, vestigial laterad, the inner end raised, almost tooth-like. Sides of pronotum converging mesad behind the crest, the posterior corners subrectangular and projecting. Promesonotal suture vestigial. Mesonotum with a small, more or less rectangular lateral tooth. Mesoepinotal suture impressed. Epinotum opaque, transverse; the basal face with a short, triangular tooth anterolaterally and a much larger, stout, strongly diverging tooth at the posterior corner, having a ventral lobe near its tip. Microsculpture as on head. Dorsum of thorax and laterotergite of pronotum covered with rather dense, deeply impressed setiferous foveolae, much larger than on upper surface of head, rounded on mesonotum, elongate on epinotum. Declivous face and posterior portion of the sides of the thorax without conspicuous macrosculpture; declivous face not crested on the sides.

Petiole opaque, transverse, anterior corners rounded; with a rather short, acute, scarcely recurved tooth on each side. Postpetiole with a plate-like lateral tooth, curving slightly foreward. Both segments finely reticulate-punctate, opaque, covered with vestigial foveolae and rugosities.

Gaster subopaque, subcordiform, about as long as wide. First gastral tergite with a narrow, semitranslucid lamellate anterolateral border; finely reticulate.

All foveolae, except on upper surface of head, contain a decumbent seta, which is flattened, shiny, and scale-like on thorax and peduncle. Erect pilosity on the terminal tergites of the gaster and the sternites. First gastral tergite beset with minute appressed setulae. Scales canaliculate on dorsum of thorax."

Measurements (in mm) and indices: TL 6.08–7.84; HL 1.56–2.12; HW 2.12–2.60; EL 0.43–0.45; PW 1.96–2.24; PeW 0.75–0.84; PpW 0.70–0.90; HBaL 0.64–0.72; HBaW 0.14–0.18; CI 122.6–135.9; PI 108.2–116.1; PPeI 261.3–266.7; PPpI 248.9–280.0; HBaI 21.8–25.0.

G y n e (Fig. 87) (previously undescribed). - Head dorsally convex. Frontal carinae converging anteriorly, their sides gently convex and ending behind the eyes. Vertexal angles obtuse. Vertex with a pair of median, stout denticles higher than the vertexal angles. Anterior clypeal border slightly concave medially and with a pair of small lateral denticles. Mandibles broad, without a lateral tumulus or denticle. Cheeks without carina.

Mesosoma. Humeral angles with a pointed anterior tooth. Pronotal carina narrow and superficially interrupted in the middle, in some specimens absent laterally. Mesonotum and scutellum flat. Lower mesopleura with a large, stout tooth. Sides of the basal face of propodeum gently convex and bearing, laterally, a pair of curved, stout, round teeth; sides of the declivous face converging posteriorly.

Petiole with the anterior face oblique and slightly concave medially; posterior face of the petiole declivous dorsally; petiolar sides gently convex, with or without a small posterior denticle. Postpetiole broadly convex, with a depression on the middle of the dorsum; anterior sides of the postpetiole with a stout, obtuse or round tooth.

Gaster with a broad, marginate, anterior lobe.

Legs. Fore coxae round anteriorly. Mid and hind femora not angulate. Hind basitarsi nearly flat and slightly broadened at their base.

Wings as in Fig. 88.

Sculpture. Head dorsum minutely reticulate-punctate and with small, superficial foveae smaller than their interspaces, the foveae more superficial and sparser on the frontal carinae. Ventral face of the head, anterior part of the pronotum and propleurae reticulate and with dense, deep, foveae larger than their interspaces. Posterior part of the pronotum, basal face of the propodeum, anterior third of the declivous face of the propodeum, upper meso- and

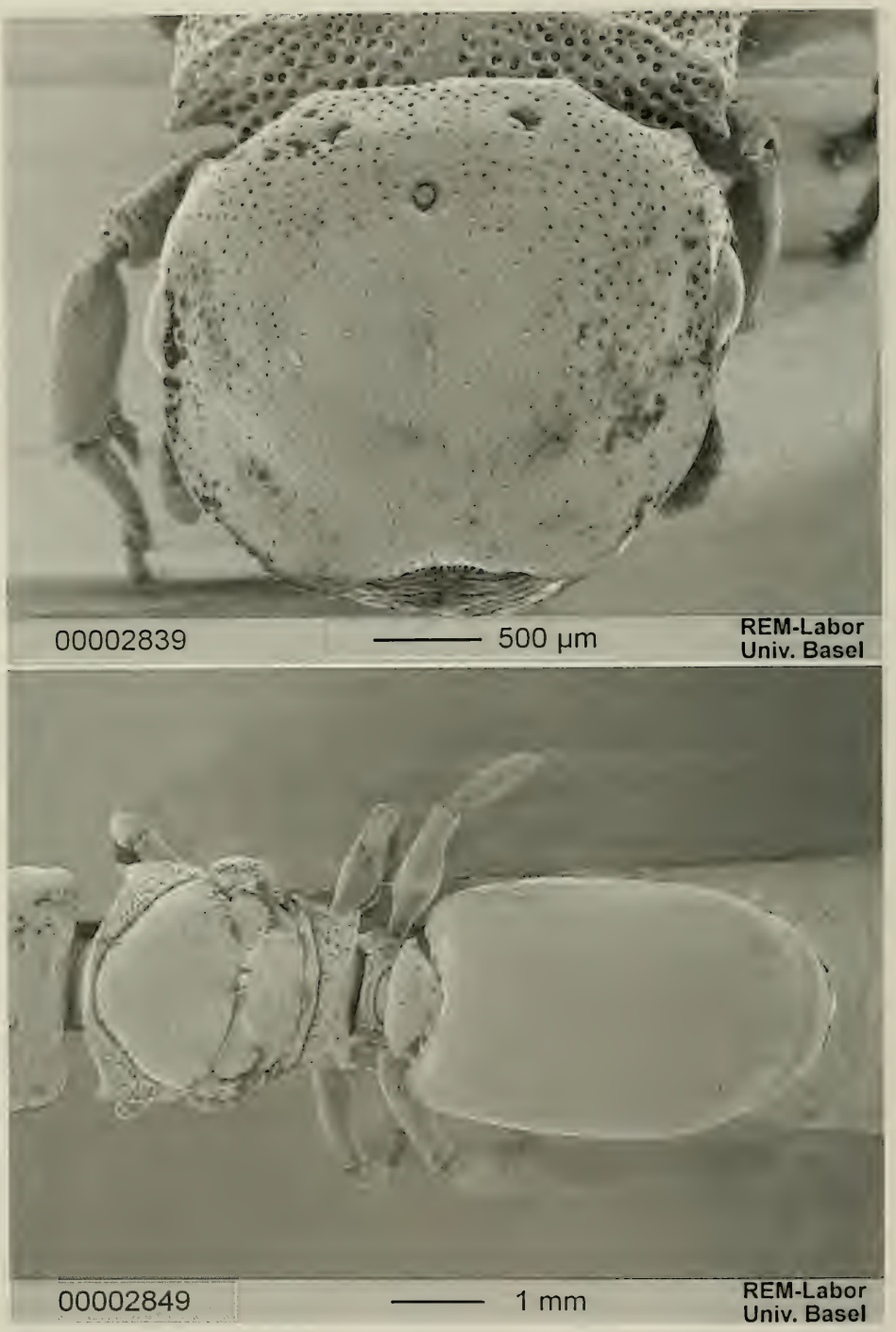


Fig. 87. *Cephalotes christopherseni* (FOREL). Gyne from Gamboa, Panama: head (top) and meso- and metasoma (bottom) in dorsal view.

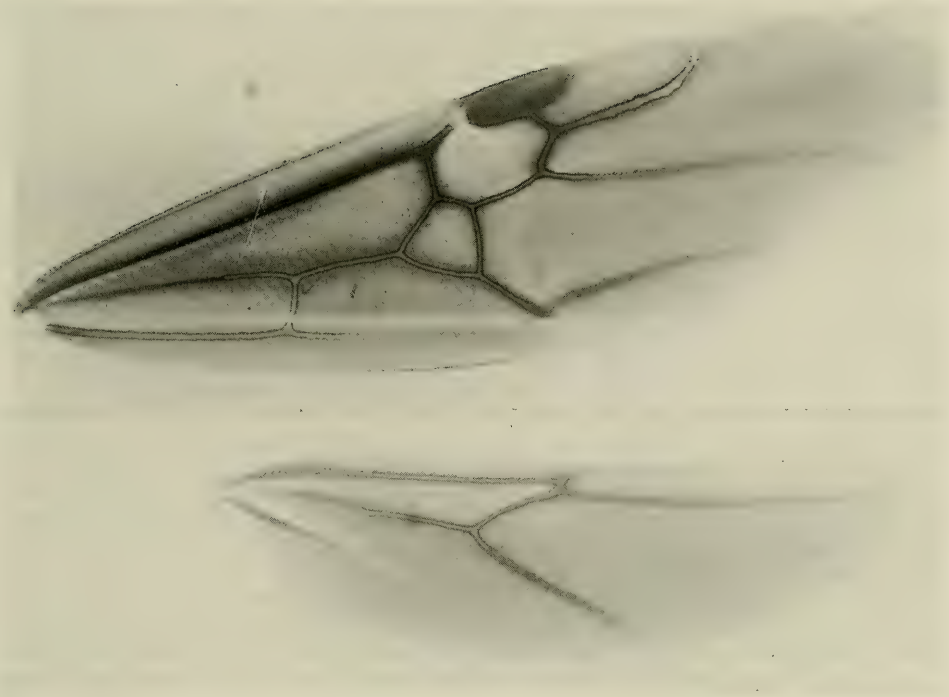


Fig. 88. *Cephalotes christopherseni* (FOREL). Gyne from Gamboa, Panama, fore and hind wings.

metapleurae, anterior half of the lower mesopleurae, sides of the petiolar dorsum and postpetiole reticulate and with dense, deep foveae smaller than on the ventral face of the head. Anterior half of the mesonotum and scutellum superficially reticulate, almost shining, with sparse foveae; posterior half of the mesonotum with dense foveae superimposed by irregular, nearly longitudinal rugulae. Middle of the petiolar dorsum, posterior half of the lower mesopleurae, lower metapleurae, two posterior thirds of the declivous face of the propodeum, gaster and legs reticulate. Gaster with sparse, superficial foveae, in some specimens the foveae denser and more impressed on the anterior third of the first gastral tergite. Extensor face of the tibiae with irregular foveae.

Pilosity. Each fovea bears a thin, appressed hair; pronotal sides and legs with rare, long, slightly clavate, suberect hairs; hairs similar to those on the pronotal sides but shorter and sparser on the first gastral tergite, denser and of the same length on the remaining gastral tergites and on the sternites. Legs and gastral segments with sparse, thin hairs similar to those arising from the foveae.

Colour. Black. Gaster, tibiae and tarsomeres dark red to brown. Frontal carinae light brown and semitransparent. Gaster with a reddish macula anteriorly.

Measurements (in mm) and indices: TL 9.82–10.90; HL 1.76–2.16; HW 2.24–2.52; EL 0.48–0.50; PW 2.08–2.48; PeW 0.79–1.00; PpW 0.81–1.20; HBaL 0.75–0.76; HBaW 0.20–0.21; CI 116.7–127.3; PI 101.6–107.7; PPeI 240.0–263.3; PPpI 200.0–256.8; HBaI 26.3–28.0.

M a l e (previously undescribed). - Head (eyes included) more than 1/3 broader than long; sides of the head strongly convex and converging towards the occiput. Vertex dorsally gently protruding. Compound eyes broadly convex. Frontal carinae short and not reaching the median ocellus posteriorly. Frons flat. Clypeus convex posteriorly and truncate anteriorly.

Mandibles short; external face without carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards, without carinae. Mesonotal scutum convex in side view; median Mayrian furrow little impressed. Basal and declivous faces of the propodeum differentiate; basal face gently convex and sloping backwards; declivous face posteriorly marked by a longitudinal, convergent carina.

Petiole with truncate anterior face; posterior face sloping posteriorly. Petiole laterally unarmed. Postpetiole, laterally, with a pair of small, median denticles.

Genitalia and subgenital plate as in Fig. 89.

Wings as in the gyne.

Gaster as broad as the mesosoma.

Sculpture. Head dorsum reticulate and irregularly rugulose, the rugae more transversal around the eyes; this sculpture superimposed to foveae, larger, slightly, irregular on the posterior third of the head, smaller, shallower and regular on the frons. Ventral part of the head reticulate and strongly rugulose. Pronotum, mesonotum, scutellum, pro- and mesopleurae minutely and superficially reticulate and covered with shallow foveae, the reticulation more impressed on the pronotum and on the propleurae. Basal face of the propodeum punctate and with irregular rugosities; declivous face of the propodeum superficially reticulate and with thin, longitudinal rugosities in the middle. Pedicel superficially reticulate and laterally covered by thin, longitudinal rugosities. First gastral tergite and sternite reticulate; the reticulation more superficial on the remaining tergites and sternites. Legs superficially and minutely reticulate and slightly shining.

Pilosity. Body with light ferruginous, flexuous, thin, pointed hairs dense on the head, on the mesosoma, on the pedicel and on the ventral face of the femora, sparser on the gaster. Gaster and legs with additional, similar hairs but shorter, appressed on the tergites, on the sternites and, on the femora, on the superior, on the external, and on the internal sides. Tibiae and tarsi with short, pointed hairs.

Colour. Black with lighter gaster. Femora, tibiae and tarsi yellow.

Measurements (in mm) and indices: TL 8.28; HL 1.12; HW 1.56; EL 0.49; PW 1.48; PeW 0.92; PpW 0.96; HBaL 0.92; HBaW 0.15; CI 139.3; PI 105.5; PPeI 160.9; PPpI 154.2; HBaI 16.3.

Material examined. - **Panama**: no further locality, 2 workers, 1 soldier (syntypes), CHRISTOPHERSEN [MHNG]; Monte Lirio, 18.XI.1911, 3 workers, 4 soldiers, W. M. WHEELER [MCZC]; Red Tank, Canal Zone, 3 workers, W. M. WHEELER [MCZC]; San Francisco, 1932, 4 workers, BIERIG [NHMB]; Juan Diaz, 1 worker, 11.VI.1930, BIERIG [NHMB]; Barro Colorado, Nature Monument, Gigante Peninsula: Enders trail, 27.III.1992, 6 workers, J. E. TOBIN [MCZC]; Barro Colorado Island, Canal Zone, 25.VI.–15.VII.1924, 2 workers, N. BANKS [MCZC]; same locality, 22.VI.1924 and 05.II.1935, 2 workers, W. M. WHEELER [MCZC, MZSP]; same locality, Aug. 1930, 2 workers, C. P. HASKINS [MCZC]; same locality, Oct.1946, Apr.-Oct. 1947, 20 workers, 7 soldiers, ZETEK [USNM]; same locality, I.1960, 7 workers, W. L. BROWN &. E. S. MCCLUSKEY [MCZC]; Gatun, 18.XI.1911, 9 workers, W. M. WHEELER [MCZC]; Cerro Campana, 09.VIII.1969, 1 worker, J. LAWRENCE B. & T. HLAVAC [MCZC]; Gamboa, 10.V.1972, 1 gyne, R. & E. FROESCHNER [USNM]; Panama City, 02.III.1983, 2 workers, 2 soldiers, 2 gynes, D. E. WHEELER [MCZC].

Colombia: Magdalena: Santa Marta, 3 workers, Forel (1 lectotype, 2 paralectotypes) [MHNG]; same locality, 1 worker, SANTSCHI [NHMB]; Sierra Nevada, 1 worker, FOREL [USNM]; Río Frío, Mar. 1924, 3 workers, 2 soldiers, W. M. MANN [MZSP]; same locality, 26.VII.1928, 2 workers, DARLINGTON [MZSP]; same locality, 1 worker, G. SALT [MCZC]. Guajira: Dibulla, 4 workers (syntypes) [MHNG, NHMB]; R. Don Diego, 25–50 m, 18.VI.1976, 2 workers, W. L. BROWN & R. C. KUGLER [MCZC]; Quebrada Guacoche, nr. Don Diego, 22.VII.1976, 1 worker, W. L. BROWN & R. C. KUGLER [MCZC]. Meta: Carinagua, 370 m, 26.II.1973, 1 worker, M. L. CORN [MZSP].

Venezuela: no further locality, XI.1939, 6 workers, ANDUZE [MCZC]; San Esteban, XI.1939, 1 worker, P. ANDUZE [USNM]. Aragua: Rancho Grande to Ocumare, 200–500 m, 25.VI.1971, 1 worker, W. L. & D. E. BROWN [MCZC]; 2 km N of Ocumare de La Costa, 31.III–2.IV.1981, 1 worker, A. S. MENKE & L. HOLLENBERG [USNM].

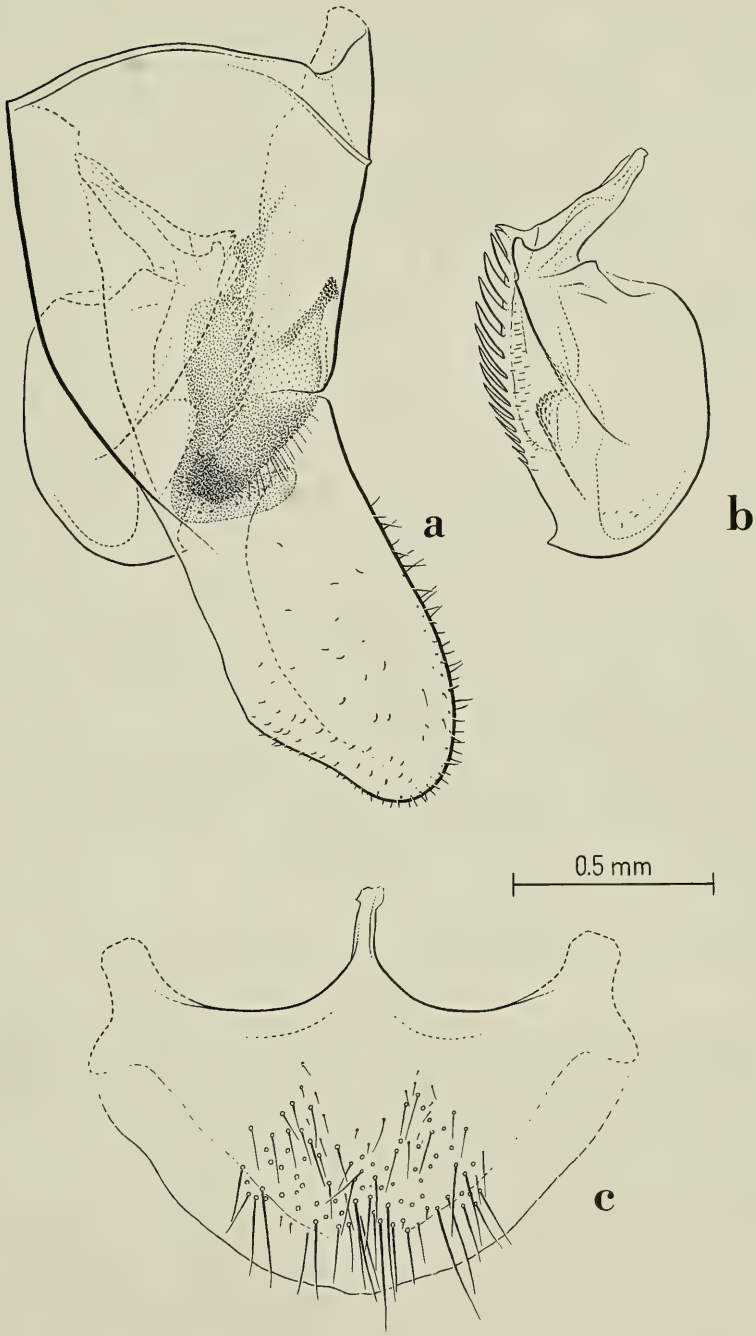


Fig. 89. *Cephalotes christopherseni* (Forel). Male from Hato Masaguaral (Guarico), Venezuela. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Anzoategui: 9 km Clarines, 02.XI.1986, 1 worker, E. M. CANCELLO, J. LATTKE & C. R. F. BRANDÃO [MZSP]. Monagas: Caicara, Riv. Orinoco, 3 workers, G. K. CHERRIE [USNM]. Cojedes: Merecure, 2 km NE H. Piñero, near El Baúl, 22–24.X.1986, 1 soldier, CANCELLO & BRANDÃO [MZSP]; Libertad, 2 workers, MAYEUL GRISOL [MNHN]; same locality, 1923, 2 workers, M. GRISOL [MNHN]; Chaparral, 10 km W H. Piñero, ca. Baúl, 22.X.1986, 4 workers, E. M. CANCELLO & C. R. F. BRANDÃO [MZSP]. Delta Amacuro: Orinoco Delta, 31.I.1935, 1 worker, N. A. WEBER [MCZC]. Zulia: El Tucuco, 45 km SW of Machiques, 05–0 6.VI.1976, 1 worker, A. S. MENKE & D. VINCENT [USNM]. Guarico: La Cruz-Ruviera, December, 1925, 2 workers, 1 soldier, 2 gynes, M. GRISOL [MNHN]; Hato Masaguaral, 44 km S of Calabozo, 11–19.V.1985, 1 gyne, 1 male, MENKE & CARPENTER [USNM]. Barinas: Río Caparo, Res. Station, 32 km E of El Canton, 03–0 5.II.1978, 4 workers, J. B. HEPPNER [USNM]. Bolívar: Ciudad Bolívar, 23–24.I.1935, 6 workers, soldier, N. A. WEBER [MCZC]. Apure: Orinoco R., 22.I.1935, 19 workers, N. A. WEBER [MCZC].

Discussion. - The workers of *christopherseni* differ from those of *inaequalis*, *laminatus* and *spinosus* (the three species resulting as ingroup in our cladistic analysis) by the shorter vertexal and gastral lamellae, from *laminatus* and *spinosus* by the shorter pronotal spines, and from *spinosus* by the presence of mesonotal spines and by the absence of golden hairs on the mesosoma. The soldier of *christopherseni* differs from the soldiers of these species by the head less shining, by the superficial carina connecting the spines on the vertex, by the gastral lamellae shorter and by the basal face of the propodeum strongly punctate and with dense, oval foveae. The gyne of *christopherseni* differs from all the others of the *laminatus* clade for having a unique gastral macula substituting the yellow spots of the other species.

FERNÁNDEZ et al. (1996) report this species also from the Colombian states of Bolívar, Caldas, Casanare, Chocó, and N. Santander.

Some of the Venezuelan workers listed above differ from the typical *christopherseni* in having a nearly unarmed petiole or very reduced petiolar spines, shorter propodeal spines, and a broader head. KEMPF (1951: 169) already referred to workers with very reduced petiolar teeth from Panama.

Distribution: Panama, Colombia, Venezuela.

Cephalotes spinosus (MAYR) new combination

Figs. 90, 91, 92

Cryptocerus quadrimaculatus KLUG, SMITH, 1854: 219, pl. 19, fig. 8. Gyne. Nec *Cryptocerus quadrimaculatus* KLUG, 1824: 215. Misidentification detected by FOREL, 1911 b: 262.

Cryptocerus laminatus SMITH, 1860: 76, pl. 4 fig. 3. Partim. Worker. Original description. Type locality: Ega (= Tefé) (Amazonas, Brazil). Type material: one syntype worker (out of three available) in BMNH labelled "*C. laminatus*, type, Sm., Journ. Ent I.76, 59 10", examined. Misidentification detected by KEMPF, 1959. The lectotype of the true *laminatus* is in OXUM.

Cryptocerus spinosus MAYR, 1862: 761. Worker. Original description. Type locality: Amazon River (Brazil). Type material: Lectotype worker in NHMW (KEMPF, 1951: 187), labelled "Pernambuco, Coll. G. Mayr, *spinosus* G. Mayr, Type", examined and one syntype worker, same data and same collection as the lectotype, equally in NHMW, examined.

Cryptocerus punctatus MAYR, 1862: 762. Soldier. Original description. Type locality: Amazon River (Brazil). Type material: not available for the present study. Synonymy by DE DALLA TORRE, 1893: 144.

Cryptocerus laminatus peruvianus FOREL, 1911 a: 297. Soldier. Original description. Type locality: Chanchamayo, 1200 m (Peru). Type material: one soldier labelled: "Chanchamayo X, Peru, 1200 m; *Cryptocerus spinosus* Mayr r. *peruvianus* Forel, soldier type; r. *Cr. peruvianus*

Forel; *Paracryptocerus spinosus peruvianus* Forel = *spinosus* Mayr, Kempf, 1967". Synonymy by KEMPF, 1967: 361.

Paracryptocerus spinosus (MAYR), KEMPF, 1951: 187, figs. 116, 117. Worker and soldier. First combination in *Paracryptocerus*.

Zacryptocerus spinosus (MAYR), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *laminatus* clade characterised in the worker by the unarmed mesonotum and by the golden hairs on the mesosoma, in the soldier by the broad gastral lamellae and by the unarmed mesonotum, and in the soldier and gyne by the frontal carinae orange and semi-transparent.

W o r k e r (Fig. 90) (description of KEMPF, 1951). - "Length 5.2 mm. Median head length 1.29 mm; Weber's length of thorax 1.68 mm. Black; the following yellowish-brown: frontal carinae, occipital lamellae, lamellate border of the first gastral tergite. Ferruginous: first and tip of terminal funicular segments, spines of thorax and peduncular segments, tips of femora, tibiae, fore tarsi, distal half of mid and hind tarsi.

Head subopaque, slightly broader than long, broadest behind the eyes, narrowed in front. Interocular distance subequal to maximum length of head (64:65). Posterior margin scarcely concave. Occipital angles with projecting, obliquely truncate lamellae, the apical border of which is sinuate. Cheeks strongly marginate beneath, densely covered with appressed, scale-like hairs. Upper and lower surface of head microscopically reticulate-punctate, sparsely covered with golden, slender, appressed scales. A few broader and canaliculate scales towards the occipital border.

Thorax subopaque. Anterior border moderately arcuate, shoulders angulate. Lateral border of pronotum with two subequal, strong, scarcely recurved and somewhat raised spines. Posterior corners of pronotum not projecting, confluent with the lateral border of the mesonotum. Promesonotal suture vestigial. Mesonotum unarmed at the sides. Thorax scarcely constricted laterad between mesonotum and epinotum. Mesoepinotal suture distinct and impressed. Basal face of epinotum, excluding the spines, about twice as long as broad, with two spines arising from its lateral border on each side. The anterior spine subequal to the prothoracic spines, the posterior spine very strong, twice as long, pointing sidewards and only slightly backwards. Microsculpture sharper, with superimposed, mostly longitudinal and rather dense rugosities on the dorsal face, between which lie rather dense, golden, canaliculate, appressed scales. Sides of thorax with longitudinal striae and sparse canaliculate scales. Declivity not excavated. Legs finely reticulate-punctate with simple, flattened hairs as on head.

Petiole subopaque, transverse, with distinctly set off, long, slender, apically recurved and rounded lateral spines, arising from the anterior corner. Postpetiole as long as, narrower than, the petiole, with shorter, broader and apically rounded lateral spines, curving obliquely forward. Sculpture of peduncle similar to head and gaster.

Gaster subopaque, cordiform, longer than broad. First gastral tergite with broad, anterolateral, transparent lamellae, the outer margin of which is slightly upturned; as broad as length of postpetiole. Tergites and sternites finely and rather sharply reticulate-punctate. Scales of gaster simple, sparse, becoming slightly denser towards the apex of the first tergite. Erect pile limited to 2d to 4th tergites and sternites."

Measurements (in mm) and indices: TL 4.80–5.80; HL 1.16–1.44; HW 1.60–1.92; EL 0.35–0.43; PW 1.28–1.60; PeW 0.68–0.76; PpW 0.60–0.68; HBaL 0.56–0.60; HBaW 0.11–0.13; CI 133.3–137.9; PI 120.0–131.2; PPeI 168.4–210.5; PPpI 191.0–235.3; HBaI 17.8–21.6.

S o l d i e r (Fig. 91) (description of KEMPF, 1951). - "Lenght 7.6 mm. Median head length 1.85 mm. Webers's length of thorax 2.22 mm. Black; the following ferruginous: frontal carinae, first funicular segment, tip of femora, tibiae apices of metatarsi, tarsi, apices of thoracic spines, peduncular spines. Lamellate border of gaster pale yellowish. Tip of last funicular segment orange.

(Head subfulgid; subquadrangular, shorter than wide; anterior corners rounded; posterior corners slightly projecting in a short, stout, bluntly rounded tooth. Frontal carinae prolonged above the eyes in the form of a distinctly raised, carinule, fading out before reaching the occi-

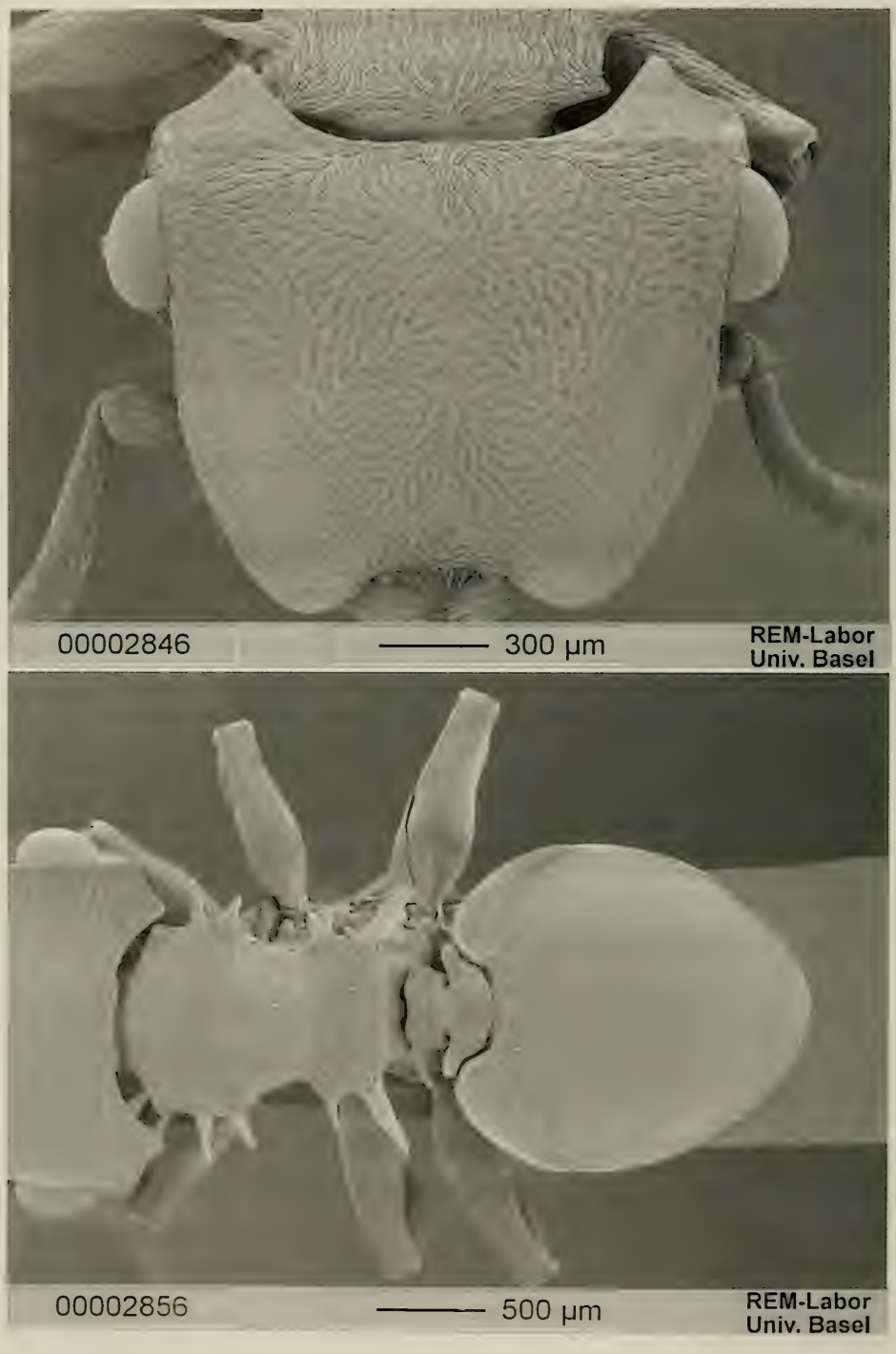


Fig. 90. *Cephalotes spinosus* (Mayr). Worker from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

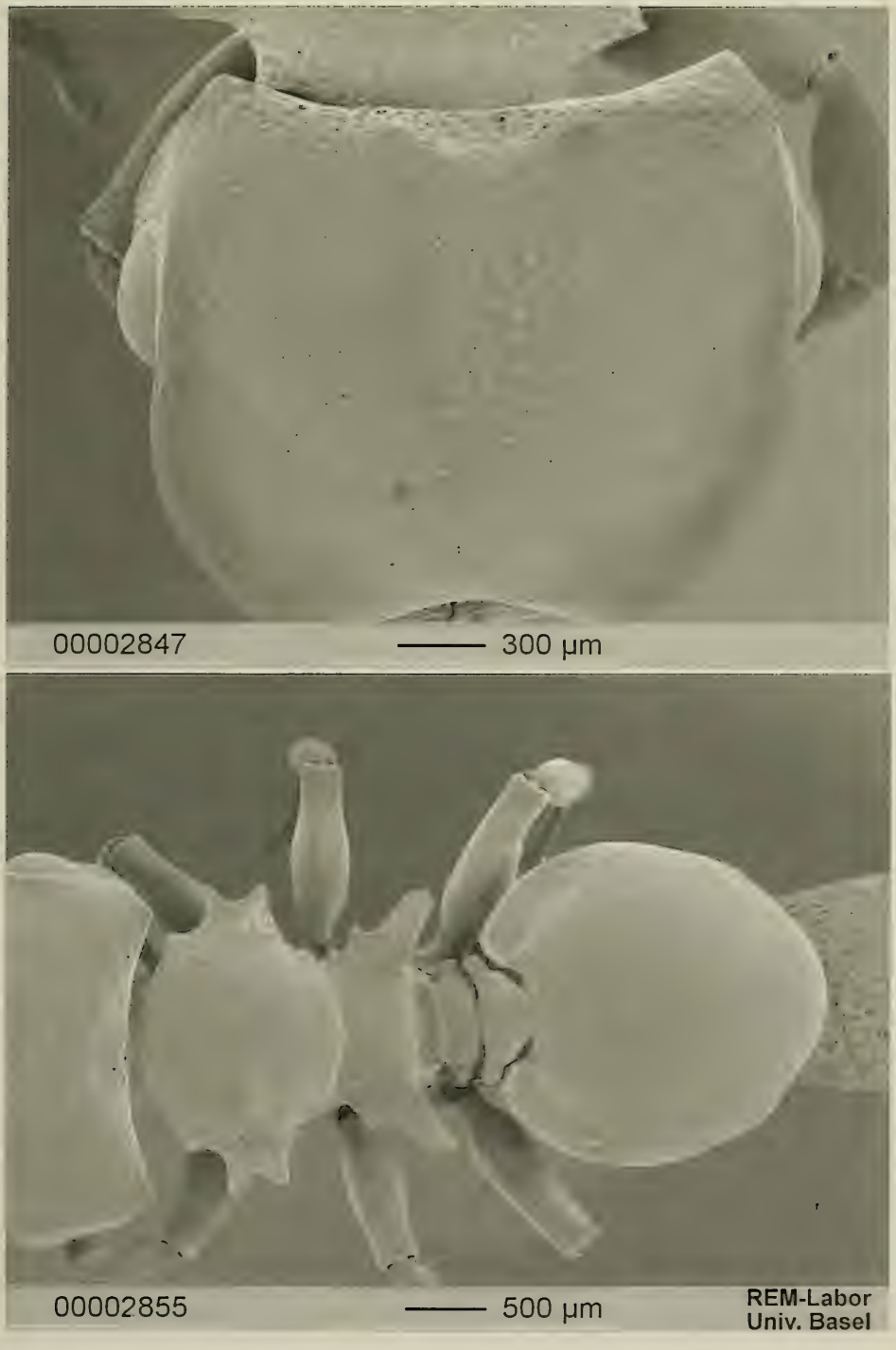


Fig. 91. *Cephalotes spinosus* (MAYR). Soldier from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

pital corner. Upper surface of head moderately convex. Cheeks not distinctly marginate beneath. Eyes little convex. A distinct carina extends from beneath the eyes back to the occipital corner. Vertex with a pair of tuberculate swellings on the immarginate occipital border. Upper and lower surface of head finely punctate, more sparsely foveolate, foveolae on upper surface of head rounded, without conspicuous hair. Occiput smooth, fulgid, sparsely foveolate.

Thorax smooth and fulgid above, sides and declivous face of epinotum opaque, finely reticulate-punctate. Anterior border arcuate, shoulders subangulate, not well visible from above. Pronotum with a transverse crest, broadly interrupted mesad, ending laterad in a stout, apically rounded, short spine, projecting outward, another spine in front of this. Sides distinctly converging cephalad and caudad from the second spine. Promesonotum, in profile, greatly convex. Promesonotal suture distinct. Mesonotum on each side with a minute, incospicuous denticule. Thorax greatly constricted between mesonotum and epinotum. Basal face of epinotum with a small triangular tooth laterad, and a large, stout, apically bluntly rounded spine, arising from the posterior corner, projecting outward and upward. Dorsum of thorax covered with rather dense, deeply impressed rounded setiferous foveolae; somewhat denser on basal face and upper third of declivous face of epinotum. Remainder of declivous face and sides of thorax without any conspicuous macrosculpture.

Petiole transverse, with a long, very slender, apically obtuse, slightly recurved spine on each side. Postpetiole with plate-like broad, rounded, lateral projection on each side. Both segments finely reticulate-punctate, opaque.

Gaster subfulgid, subcordiform, finely and densely punctured with sparse, very shallow, vestigial foveolae. Anterolateral border of first gastral tergite with a subtranslucid, excavated broad lamellate crest, as in worker.

Pilosity scarcer than in worker. All foveolae except the ones on the upper surface of head, contain a small, distinctly visible, decumbent, flat seta, which is more or less glistening on epinotum. Gaster with minute appressed setulae. Erect pile confined to the apical portion of the gaster as in other species."

Measurements (in mm) and indices: TL 6.62–8.00; HL 1.66–2.04; HW 2.28–2.72; EL 0.50–0.52; PW 1.84–2.32; PeW 0.91–0.96; PpW 0.80–0.90; HBaL 0.68–0.72; HBaW 0.16–0.19; CI 131.4–137.3; PI 115.5–123.9; PPeI 191.7–254.9; PPpI 224.4–260.7; HBaI 22.2–26.4.

G y n e (Fig. 92). - Head almost round, dorsally convex. Frontal carinae surpassing the posterior border of the eyes posteriorly as a thin margin. Vertexal angles with a pair of small, triangular teeth. Vertex with a pair of small, median, stout teeth. Clypeus concave anteriorly and with a pair of small lateral denticles. Eyes convex. Mandibles broad, without tumulus and denticles.

Mesosoma. Scapular angles visible in dorsal view. Humeral angles with a pair of pointed anterior spines. Pronotal carina superficially marked, interrupted in the middle, and absent laterally in some specimens. Mesonotum and scutellum flat. Lower mesopleurae with a variably developed, stout tooth. Sides of the basal face of the propodeum with or without a small pair of swellings followed by a long spine directed backwards; sides of the declivous face converging posteriorly.

Petiole with the anterior face concave and oblique medially; petiolar sides gently diverging posteriorly, unarmed or with a small pair of denticles medially. Postpetiole broadly convex dorsally; sides of the postpetiole with stout and round expansions.

Gaster anteriorly with a pair of broad, variably protruding, marginate lobes.

Legs. Fore coxae tumuliform anteriorly. Mid and hind femora not angulate. Hind basitarsi not flat and with almost parallel sides.

Sculpture. Head dorsum minutely and superficially reticulate-punctuate and with small, variably clumped, superficial foveae. Ventral face of the head, pronotum and scutellum smooth and with dense, deep, foveae larger than their interspaces; propleurae with similar sculpture but more impressed and superficially reticulate. Mesonotum smooth and with sparse, shallow foveae. Basal face and anterior half of the declivous face of the propodeum, upper metapleurae, petiolar sides and postpetiole with dense, deep, slightly irregular foveae. Lower meso- and metapleurae reticulate and with variably clumped foveae. Posterior half of

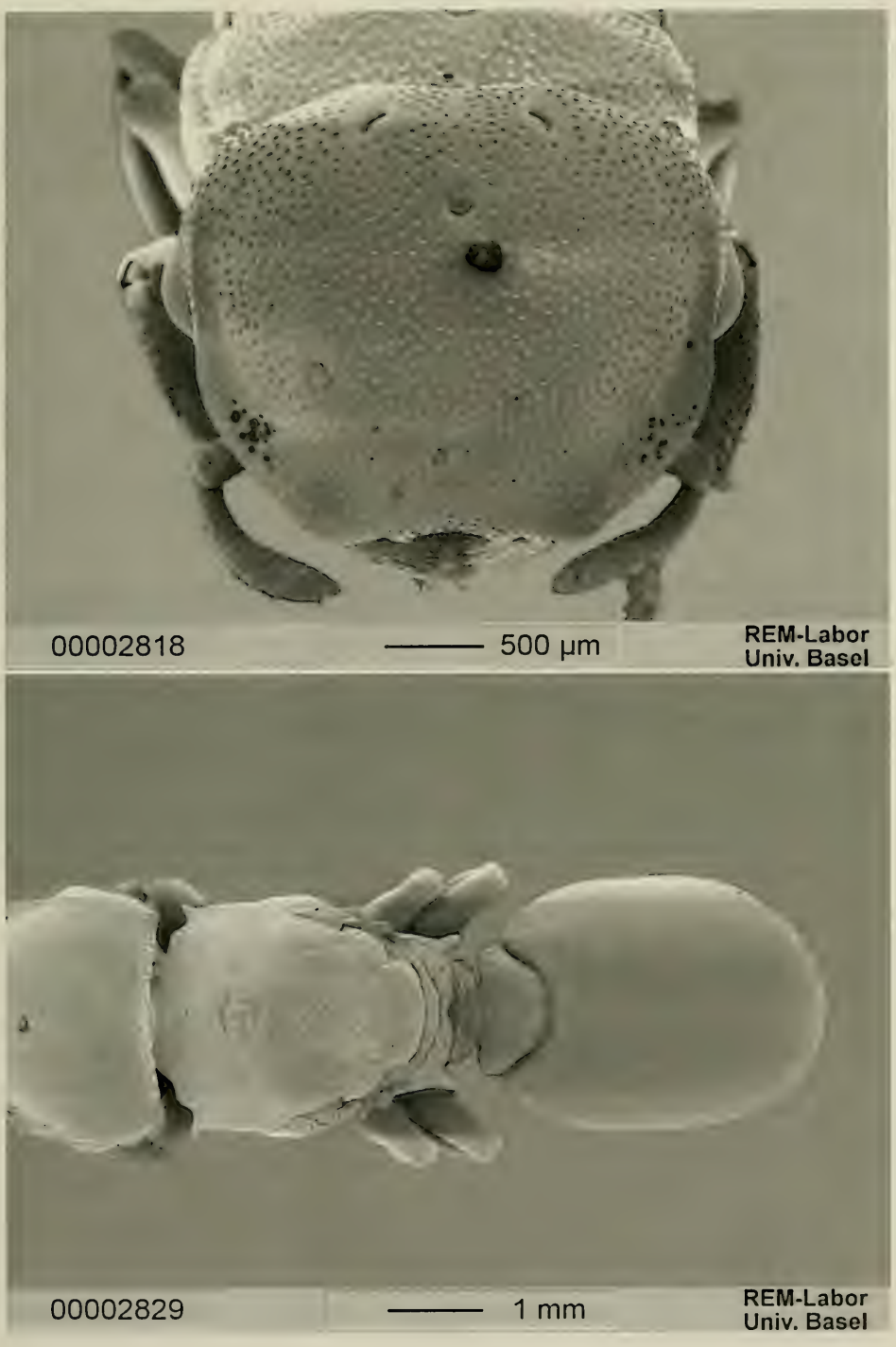


Fig. 92. *Cephalotes spinosus* (MAYR). Gyne from S. Antonio, Bolivia: head (top) and meso- and metasoma (bottom) in dorsal view.

the declivous face of the propodeum reticulate. Gaster smooth or superficially reticulate. Anterior third of the first gastral tergite with sparse, superficial foveae. Legs reticulate. Extensor face of the tibiae with small, irregular foveae.

Pilosity. Body with four type of hairs: (1) short, thin, appressed originating from a fovea on the head and on the mesosoma, or arising from very superficial foveae on the gaster and on the legs; (2) long, rare, slightly clavate on the pronotal sides, on the pedicel, on the first tergite and on the legs; (3) similar to type (2) but truncate on the remaining tergites; (4) long, dense and pointed on the sternites.

Colour. Black, slightly shining. Frontal carinae yellow-orange and transparent. Femora dark orange. Gaster with two pairs of yellow spots, one on the anterior third and the other larger and on the posterior third.

Measurements (in mm) and indices: TL 11.58–12.06; HL 2.12–2.34; HW 2.68–2.84; EL 0.56; PW 2.48–2.60; PeW 1.04–1.28; PpW 1.36–1.40; HBaL 0.80–0.87; HBaW 0.20–0.24; CI 121.4–126.4; PI 108.1–109.2; PPeI 203.1–238.5; PPpI 182.3–185.7; HBaI 25.0–27.6.

Material examined. - **Trinidad & Tobago**: Trinidad: without further locality, Jul. 1920, 5 workers [MCZC]. Nariva: near Río Claro, B. W. I., 01.VI.1936, 14 workers, 2 soldiers, N. A. WEBER [MCZC].

Colombia: Meta: Res. Nac. Nat. La Macarenã, Canõ La Curia, 580 m, 31.XII.1986, 2 workers, F. FERNÁNDEZ [MZSP]. Amazonas: La Chorrera, 30 km downhill Río Igara Paraná, 28.IX.1973, 10 workers, 3 soldiers, J. DESPLATS [MNHN]; same locality and collector, 12.II.1974, 3 workers [MNHN].

Venezuela: Apure: Low Sarare river, 1 gyne, E. GEAY [MNHN].

Guyana: no further locality, 29.III.1901, 1 worker, 1 soldier, R. J. CREW [USNM]. Essequibo: Forest Settlement, Río Mazuruni, Aug. -Nov. 1935, 2 workers, 1 soldier, N. A. WEBER [MCZC]; Oko, Río Cuyuni, 25.VI.1936, 1 worker, N. A. WEBER [MCZC]; Upper Essequibo, 01.XII.1935, 1 worker, I. G. MYERS [MCZC]; Kartabo, Jul. -Aug., 1920, 48 workers, 9 soldiers [MCZC]; New River, 10.XII.1935, 1 worker, J. MYERS [MCZC].

Ecuador: Pastaza: El Puyo, 900 m, 12.4.1958, 2 workers, W. WEYRAUCH [MZSP]. Napo: 00°24' S, 76°36' W, Limoncocha, 02.VII.1970, 1 worker, G. NAUMANN [MZSP]; 00°24' S, 76°36' W, 27.VII.1973, 2 workers, L. MORALES [MZSP].

Peru: no further locality, 17.IX.1965, 1 worker, J. C. HITCHCOCK [USNM]; Chanchamayo, 1200 m, 1 soldier (type of *spinosus peruvianus*), [MHNG]; Valle Chanchamayo, 800 m, 10.VIII.1957, 5 workers, 1 soldier, W. WEYRAUCH [MCZC, MZSP]; Valle Chanchamayo, 900 m, 01.I.1959, 1 worker, W. WEYRAUCH [MCZC, MZSP]. Huánuco: Tingo Maria, Río Huallaga, 670 m, 27.VII.1955, 3 workers, W. WEYRAUCH [MZSP].. Junín: Victoria, Jul. 2, 1 worker, W. F. WALKER [MCZC]. Cuzco: Quincemil, 750 m, Set. 1962, 1 soldier, L. PEÑA [MCZC]; Urubamba, 01–05.VI.1983, 1 worker [MZSP].

Brazil: Roraima: Auaris, 10.VII.1976, 1 worker [MZSP]. Amazonas: no further locality, 2 workers, 2 soldiers, 1 gyne (problably syntypes or nidotypes of *spinosus*), H. W. BATES [MHNG, ZSMC]; Rio Tototobi, Mar. 1976, 1 worker, A. SHELLEY [MZSP]; São Gabriel, Cachoeria, Morro e Lagos, 20.IX–0 6.X.1990, 300 m, 1 worker, J. A. VIDAL & J. VIDAL [INPA]; Res. Florestal A. Ducke, 05.X.1981, 1 worker, J. A. RAFAEL [INPA]; Manaus, km 44/45, BR–174, 27.VII.1981, 2 workers [INPA]; same locality, BR. 174, km 45, 29.VIII.1992, 85 workers, 3 soldiers [INPA]. Pará: Itaituba, Parque Nacional da Amazônia, 11.XI.1978, 9 workers, 1 soldier, R. B. NETO [MPEG]; Caldeirão, Rio Itacaiunas, Jul. Aug. 1985, 1 worker, C. R. F. BRANDÃO & W. BENSON [MZSP]; Jacareacanga, Out. 1959, 2 workers, M. ALVARENGA [MZSP]. Acre: Cruzeiro do Sul, Jul. 1973, 3 workers, T. ZIMMERMANN [MZSP]; same locality, 07.VI- 14.VII.1983, 4 workers, R. H. PIRES [MZSP]; same locality, 12.VII–18.VIII.1983, 2 workers, F. H. CAETANO [MZSP]; Rio Branco, Parque Zoobotânico Cidade Universitária, 28.II.1987, 8 workers, 1 soldier, E. DE DEUS [MZSP]; Rio Branco, 16.V.1952, 1 worker, M. ALVARENGA [MZSP]; same locality, 25.X–8.XI.1991, 1 worker, F. RAMOS et al. [MPEG];. Rondônia: Porto Velho, Rio Madeira, 12 workers, MANN & BAKER [MCZC]; Vila Rondônia, (378 km S of Porto Velho), I-II.1961, 2 workers, F. S. PEREIRA & A. MACHADO [MZSP]. Bahia: Ouro Preto do Oeste, CEPLAC, cacao

plantation, 1 worker, 2 soldiers, O. TREVISAN [CPCC]. Mato Grosso: Vila Vera, X.1973, 2 workers, M. ALVARENGA [MZSP].

Bolivia: without further locality, Apr. 1913, 2 workers, STAUDINGER [MCZC, MZSP]. Beni: Rurrenabaque, Oct. 1921, 4 workers, W. M. MANN [MZSP]; San Antonio, 06.VIII.1946, 1 worker, 2 soldiers, 2 gynes, H. MARCUS [MZSP]. La Paz: Mapiri, 1 worker [MCZC]; Tipuani, 24.X.1890, 3 workers, A. V. LEONHARD [MHNG].

Discussion. - The worker and soldier of *C. spinosus* are the sole neuter castes without mesonotal spines in the *laminatus* clade. A soldier from Ouro Preto do Oeste (Bahia) has mesonotal spines comparable to those of the other species of the clade. Since all the other soldiers we examined are regularly without mesonotal spines we regard the Bahian specimen as aberrant.

FERNÁNDEZ et al. (1996) report this species also from the Colombian state of Caquetá.

Distribution: Trinidad, Colombia, Venezuela, Guyanas, Peru, Ecuador, Brazil, Bolivia.

Cephalotes inaequalis (MANN) new combination

Fig. 93

Cryptocerus inaequalis MANN, 1916: 449. Worker. Original description. Type locality: Abunã (Rondônia, Brazil). Type material one worker (syntype) labelled: "Rio Madeira, Abuna, Brazil, Mann & Baker", in MCZC, examined.

Paracryptocerus inaequalis (MANN), KEMPF, 1951: 163, fig. 124. Worker. First combination in *Paracryptocerus*.

Paracryptocerus inaequalis (MANN), KEMPF, 1959: 96.

Zacryptocerus inaequalis (MANN), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *laminatus* clade differing from its sister species *laminatus*, in the worker, by the head shorter and broader and by the pronotal and propodeal spines shorter and thicker, and, in the soldier, by the head broader, with parallel frontal carinae less converging anteriorly, and by the sculpture more superficial and opaque, and, in the gyne, by the head, flatter and broader.

Worker (Fig. 93) (description of KEMPF, 1951 & 1959). - "Length 5.5 mm. Median head length 1.29 mm; Weber's length of thorax 1.63 mm. Black; the following pale yellowish-brown and semitranslucid: frontal carinae, occipital lamellae, thoracic and peduncular spines; lamellate border of the first gastral tergite. Ferruginous: tibiae, tarsi, apices of mandibles. Fuscous: femora and base of mid and hind basitarsi.

Head subopaque; broader than long, broadest behind the eyes, narrowed in front; interocular distance longer than maximum length of head (78:74). Posterior margin between the lobes, scarcely concave, almost straight, the occipital angles with prominently projecting, obliquely truncate lamellae, the apical border of which is distinctly sinuate. Cheeks strongly marginate beneath, covered with dense, large, canaliculate, golden scales. Integument very finely reticulate-punctate, sparsely covered with slender, simple, short, appressed, scale-like hairs which, near the occipital border, are situated in grooves.

Thorax subopaque. Pronotum angulate at the shoulders; broadly expanded behind the shoulders with two broad, flat, triangular teeth on each side; posterior corners of pronotum more or less rounded and projecting. Promesonotal suture obsolete. Mesonotum with a small, acute, lateral tooth. Mesoepinotal suture impressed. Basal face of epinotum with two large, broad, flat, triangular teeth on each side, the anterior tooth sligtly smaller than the posterior. The posterior border of the second tooth forms a sharp crest and delimits the distinctly excavated declivous face laterad. Sculpture as on head, but sparsely foveolate above, with very short, broad scales, some of which are distinctly canaliculate, becoming slightly longer on the basal face of the epinotum. Laterotergite of pronotum and mesopleura longi-

tudinally striated. Excavated portion of declivous face without distinct macrosculpture and without scales.

Petiole subopaque, transverse, with set off, slender, long, lateral spines, arising from the anterior corner, gently curved backwrds, rounded at apex. Postpetiole with somewhat shorter, broader lateral spines, bluntly rounded at apex, curving obliquely foreward. Sculpture as on thorax, less distinctly foveolate, scales slightly longer.

Gaster subopaque; broadly cordiform, very convex above. First gastral tergite with anterolateral, flat, lamellate border, almost as broad as the length of petiole. Tergites and sternites finely, densely and rather sharply reticulate-punctate. Scales of gaster sparser, simple, short, not situated in distinct foveolae. Erect pile limited to the 2nd – 4th gastral tergites and the sternites."

Measurements (in mm) and indices: TL 4.89–5.68; HL 1.20–1.42; HW 1.64–2.04; EL 0.38–0.44; PW 1.28–1.52; PeW 0.66–0.86; PpW 0.55–0.74; HBaL 0.51–0.60; HBaW 0.12–0.13; CI 135.5–143.7; PI 123.5–134.2; PPeI 176.7–200.0; PPpI 205.4–232.7; HBaI 21.7–25.0.

S o l d i e r (previously undescribed). - Head subquadrate, convex dorsally. Frontal carinae anteriorly gently converging, straight laterally and terminating behind the eyes. Vertexal angles round or obtuse. Vertex with a pair of median small, stout teeth. Mandibles broad, short and without lateral angle.

Mesosoma. Scapular angles visible. Pronotal sides anteriorly with a pair of broad, bidentate lamellae; first pair of lamellar teeth pointed and the second one round or truncate; pronotal sides converging posteriorly. Pronotal carina marked, interrupted in the middle by a notch. Promesonotal suture impressed. Mesonotal sides with a pair of broad, truncate teeth. Propodeal suture impressed. Propodeum with clearly differentiate basal and declivous faces. Basal face plate-like, its sides diverging posteriorly and with a pair of triangular teeth followed by a pair of spines; propodeal spines diverging backwards, with the base continuing into the anterior half of the declivous face. Declivous face of the propodeum converging posteriorly.

Petiole with the anterior face obliquely truncate. Petiolar sides with a pair of thick spines arising anteriorly and curved backwards. Postpetiole slightly narrower than the petiole and convex dorsally. Postpetiolar spines originating from the anterior face, slightly directed forwards and with almost round tips.

Gaster oval, with a pair of broad lamellae reaching at least the stigma posteriorly.

Legs. Fore coxae tumuliform anteriorly. Mid and hind femora without angles or denticles. Mid and hind basitarsi not flat and with parallel sides.

Sculpture. Head dorsum minutely and superficially punctate, subopaque and covered by faint, small foveae smaller than their interspaces. Frontal carinae superficially shining and with foveae sparser than those on the remaining head dorsum. Ventral part of the head posteriorly shining and with deeper and larger foveae than on the head dorsum, and anteriorly punctate and with foveae denser and smaller than on the posterior half. Pronotum and mesonotum minutely and superficially punctate, slightly shining and with foveae larger and deeper than those on the on the head dorsum. Basal face of the propodeum and anterior third of the declivous face punctate and densely foveolate, the foveae deeper than on the other mesosomal parts. Propleurae punctate and with large, variably clumped, foveae. Meso- and metapleurae punctate and with rare, superficial foveae. Pedicel punctate and with dense, irregular foveae, shallower than those on the basal face of the propodeum. Declivous face of the propodeum, gaster legs and reticulate-punctate, the reticulation broader and more superficial on the legs. Outer face of the femora with irregular, thin rugosities between superficial, irregular foveae. First gastral tergite with superficial foveae diminishing in size and shallower posteriorly. Anterior and posterior faces of the femora, and centre of the first gastral sternite shining. Some specimens shining on the first gastral tergite as well. Posterior half of the first gastral sternite centrally superficially reticulate-punctate, almost shining.

Pilosity. Each fovea bears an appressed hair. Gastral sternites and legs with thin, appressed hairs. Posterior border of the gastral tergites and of the sternites, and legs with clubbed hairs. Sternites with additional rare, pointed, long hairs.

Colour. Black. Frontal carinae anteriorly with a ferruginous, semitransparent spot. Lamellaceous border of the gaster yellow ferrugineous and semitransparent. Gaster with or

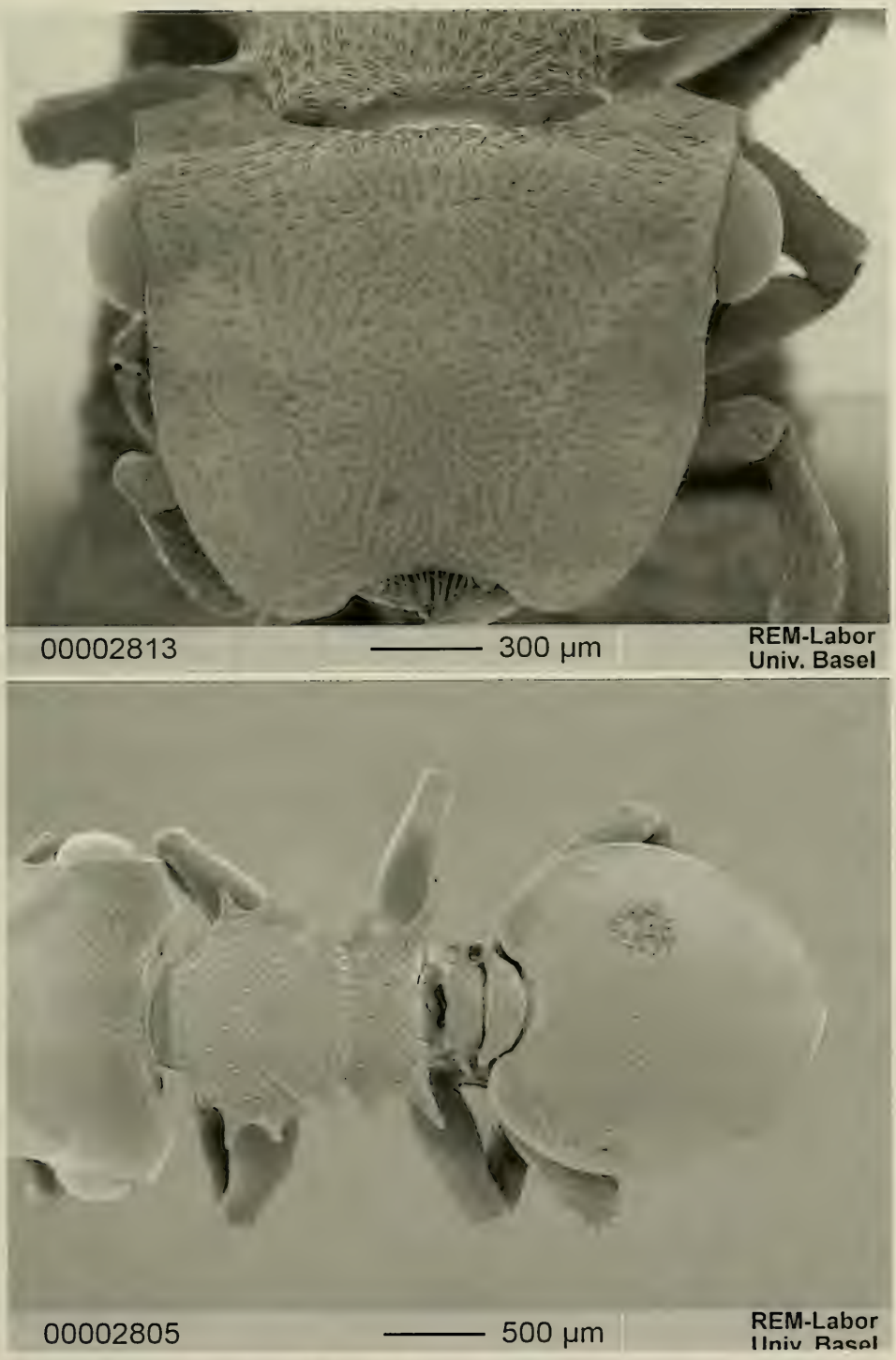


Fig. 93. *Cephalotes maequalis* (MANN). Worker from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

without a small pair of orange spots anteriorly. Tibiae and tarsomeres orange to dark ferrugineous.

Measurements (in mm) and indices: TL 7.08–7.98; HL 1.80–2.12; HW 2.40–2.64; EL 0.48–0.54; PW 2.00–2.16; PeW 0.78–0.93; PpW 0.80–0.85; HBaL 0.59–0.65; HBaW 0.16–0.17; CI 123.5–135.0; PI 116.7–122.2; PPeI 229.8–246.1; PPpI 234.1–254.1; HBaI 24.0–27.4.

Gyne (previously undescribed). - Head broader than long, more convex than in the soldier. Frontal carinae gently converging anteriorly; their sides parallel and ending behind the eyes. Vertexal angles obtuse and reaching the ventral border of the eyes anteriorly. Vertex with a pair of median, small teeth connected each other by a weak median carina. Clypeus anteriorly concave, with a pair of small lateral teeth. Eyes gently convex. Mandibles as in the soldier.

Mesosoma. Scapular angles short but visible. Humeral angles with a pair of pointed anterior teeth. Pronotal sides straight. Pronotal carina narrow, superficially marked and interrupted in the middle. Mesonotum and scutellum flat. Lower mesopleurae with a small denticle. Basal face of the propodeum anteriorly with a pair of minute denticles and with a pair of pointed teeth. Declivous face with the sides converging posteriorly.

Petiole as in the soldier. Postpetiole as in the soldier but with thicker and slightly truncate spines.

Gaster with a pair of broad, strongly marginate anterior lobes.

Legs. As in the soldier.

Sculpture. As in the soldier but differing in the following: ventral part of the head punctate and with deep and dense foveae. Posterior part of the mesonotum and scutellum with dense foveae separated by longitudinal interspaces. Propleurae with denser and deeper foveae. Upper metapleurae with dense, small foveae. Lower mesopleurae and upper metapleurae with variably clumped foveae. Lower metapleurae with thin, longitudinal rugosities on the ventral part, the rest punctate. First gastral tergite superficially reticulate on the anterior third, the rest superficially punctate and shining. Remaining tergites and sternites reticulate. Centre of the first gastral sternite shining. Foveae on the gaster more impressed.

Pilosity. As in the soldier but with the clubbed hairs sparse and present also on the mesosoma, on the pedicel, and on the gaster

Colour. Black. Frontal carinae with two pairs of ferruginous and semitransparent spots. Gaster with two pairs of orange spots, the first pair on the anterior third and the second ones before the posterior border of the first tergite. Tibiae and tarsomeres orange to dark ferruginous.

Measurements (in mm) and indices: TL 12.18; HL 2.48; HW 3.02; EL 0.56; PW 2.78; PeW 1.16; PpW 1.54; HBaL 0.80; HBaW 0.23; CI 121.8; PI 108.6; PPeI 239.6; PPpI 180.5; HBaI 28.7.

Material examined. - **Brazil**: Amazonas: Tefé, XII.1961, 1 gyne, F. M. Oliveira [MZSP]; Manaus, Res. Ducke, 28.II.1978, 2 workers, 1 soldier, J. Arias & N. Penny [INPA]; same locality, 14.II.1978, 3 workers, J. Arias [INPA]; same locality, 26.VIII.1982, 1 worker, Adis et al. [INPA]; same locality, 01–0 2.XI.1983, 1 small soldier, C. Bordon [INPA]; same locality, 22–26.I.1996, 4 workers, M. L. de Andrade [INPA]; same locality, 13& 20.IX.1977, 3 workers [MPEG]; BR–174, km 44, EEST/INPA, 27.II.1983, 1 worker, A. Y. Harada [INPA]; Manaus, 2F3, km 24, Fazenda Esteio, Florestal, 21.III.1983, 1 worker, A. Y. Harada [MZSP]; same locality, Res. WWF, 22.III.1983, night, 1 worker, A. Y. Harada [INPA]; Manaus, Reserva Campina, 28.VII.1977, 1 worker [INPA]. Pará: Marajó-Breves, Rio Caruacá, 6.VIII.1988, 2 soldiers, J. Dias [MPEG]; Vigia, 9.XII.1988, 1 worker, W. França [MPEG]; Benevides, Fazenda Morelândia, VI-VII.1988, 6 workers, F. F. Ramos [MPEG]; Serra Norte, Salobo, 26.VI.1984, 2 workers, M. Zanuto [MPEG]; Jacareacanga, X.1959, 1 soldier, M. Alvarenga [MZSP]. Rondônia: Ouro Preto do Oeste, different dates and collectors, 26 workers [MPEG]; Abunã, Rio Madeira, 1 worker (syntype), Mann & Baker [MCZC]; Teixeirópolis, 22.XI.1995, 1 worker, A. Y. Harada [INPA]. Mato Grosso: Aripuanã, Est. Pontanilha, 27.I.1976, 1 soldier, L. P. Albuquerque [INPA]; Sinop 55° 37' W 12° 31' S, X–1974, 1 worker, M. Alvarenga [MZSP].

D i s c u s s i o n . - KEMPF (1951, 1959), without knowing the soldiers, stressed the similarities between *inaequalis*, *laminatus* and *christopherseni* and expressed some doubts about their specific validity. C. *inaequalis* is very similar to *laminatus*. Their diagnostic characters are given in the respective diagnoses. The discovery of the soldier and of the gyne of *inaequalis* confirms the validity of its specific status by adding the characters of these castes already listed in the diagnosis.

C. *inaequalis* and *laminatus* are sympatric in many areas on NW of Brazil. The separation of the two species has been facilitated by the examination of workers associated with soldiers. C. *christopherseni* (q. v.) belongs to the same subclade as *inaequalis* but is much closer to *spinosus*.

FERNÁNDEZ et al. (1996) report this species from the Colombian states Amazonas and Caquetá.

D i s t r i b u t i o n : Brazil (and Colombia?).

Cephalotes laminatus (SMITH) new combination

Figs. 94, 95, 96, 97

Cryptocerus laminatus SMITH, 1860: 76, pl. 4, fig. 3. Worker. Original description. Type locality: Ega (= Tefé) (Amazonas, Brazil). Type material: lectotype worker without locality label in OXUM (Type Hymenoptera 1042) (designated by KEMPF, 1959: 95), examined; possible additional type material or material from the same series not examined by Smith: one worker and one soldier labelled "Amazonas, H. W. Bates S." in the ZSMC (FOREL, 1911 b: 261), examined; second worker labelled "Amazonas, H. W. Bates S., cotype" in MHNG, examined.

Paracryptocerus laminatus (SMITH), KEMPF, 1958 a: 164, fig. 3. Worker. First combination in *Paracryptocerus*.

Paracryptocerus laminatus (SMITH), KEMPF, 1959: 95, fig. 3. Worker.

Zacryptocerus laminatus [?], OLIVEIRA, 1985: fig. 7. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the homonymous clade differing from its sister species, *inaequalis*, in the worker, by the head longer and narrower, by the pronotal and propodeal spines longer and thinner, and, in the soldier, by the head narrower with the frontal carinae strongly converging anteriorly and by the sculpture more impressed and shining, and, in the gyne, by the head more convex and narrower.

W o r k e r (Fig. 94) (translation of the description of KEMPF, 1958 a). - "Total length 5.3 mm; maximum head length 1.48 mm; median head length 1.19 mm; thorax length 1.52 mm.

Differs from *inaequalis* (Mann, 1916) for the following characters: semitransparent lamellae of the head and of the gaster and thoracal and petiolar spines darker, i. e. light ferruginous. Border of the occipital lamellae slightly curved, near straight. Lateral pronotal teeth less flat and widened at the base. Promesonotal suture vestigial. Mesoepinotal suture superficially impressed. Lateral epinotal teeth like those of the pronotum, with the posterior distinctly longer than the anterior one. Thoracic dorsum with denser foveolae and longer scales in the foveolae. Gaster much longer than wide, the median length larger than the maximum width with a proportion of 54:47; anterolateral lamellae narrower; scales longer.

Can be distinguished from *christopherseni* (FOREL, 1912) for the following characters: Lighter tibiae. Head longer than the thorax, less flat in its superior face. Maximum diameter of the eyes exactly 1/3 of the head length. Second lateral pronotal tooth as long as the first, wider at the base; lateral border of the pronotum between the point of the second teeth and the posterior angle very weakly curved. Epinotal teeth thicker. Declivous face of the epinotum excavated in the middle, with the lateral borders strongly carinate."

Measurements (in mm) and indices: TL 4.65–5.28; HL 1.16–1.26; HW 1.56–1.72; EL 0.38–0.44; PW 1.16–1.32; PeW 0.62–0.65; PpW 0.52–0.64; HBaL 0.48–0.56; HBaW 0.11–0.12; CI 133.3–138.7; PI 130.0–137.1; PPeI 183.3–200.0; PPpI 188.6–238.5; HBaI 19.6–23.1.

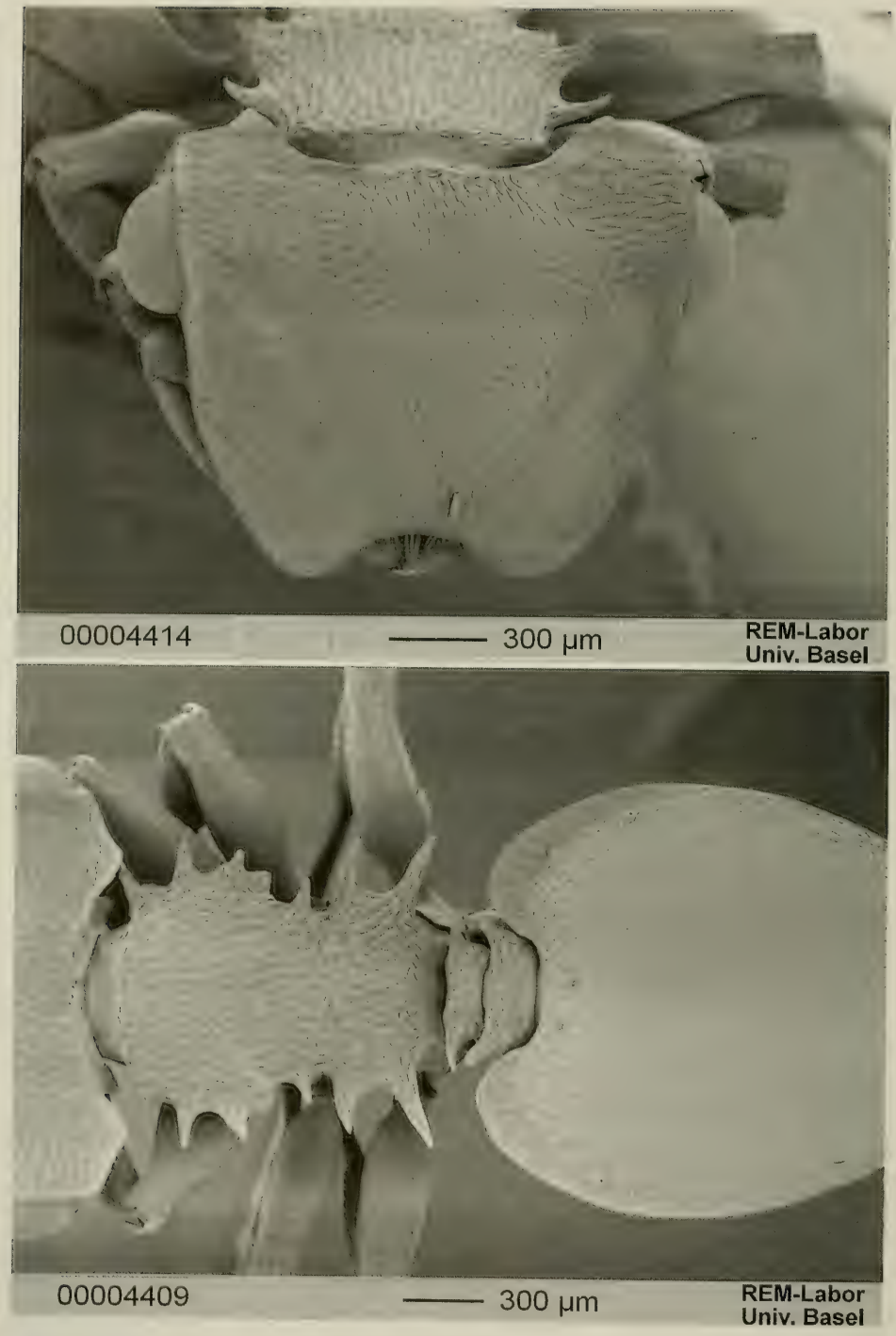


Fig. 94. *Cephalotes laminatus* (SMITH). Worker from Mato Grosso, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

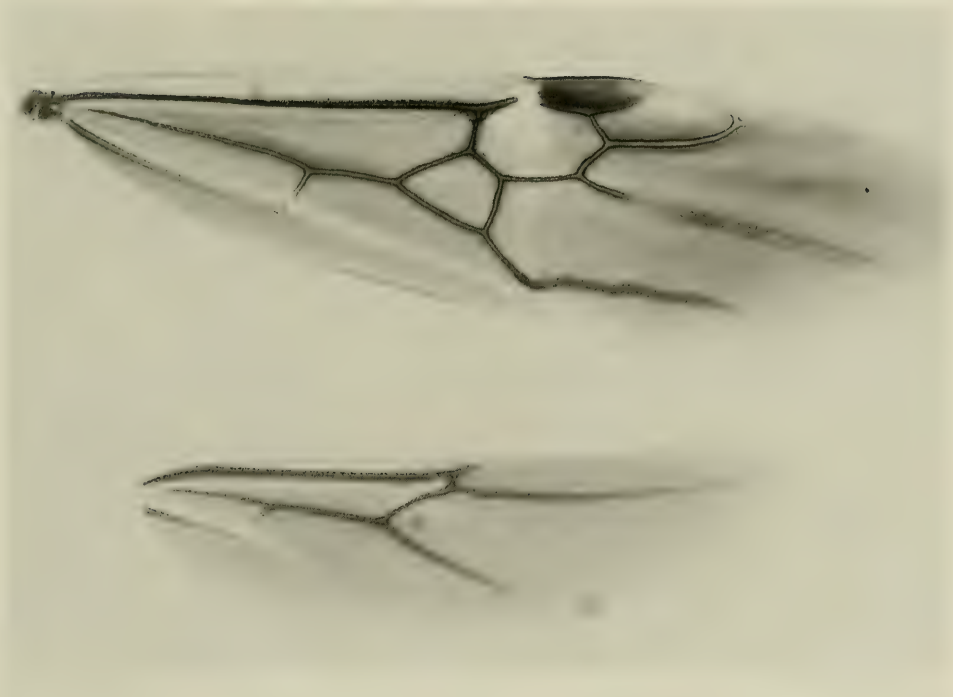


Fig. 95. *Cephalotes laminatus* (SMITH). Gyne from Manaus, Brazil, fore and hind wings.

S o l d i e r (previously undescribed). - Differing from *inaequalis* in the following: frontal carinae anteriorly strongly converging towards the mandibles, laterally straight and gently upturned, and not reaching the posterior border of the eyes.

Mesosoma. Pronotal sides with the first pair of lamellar teeth more acute and broader. Mesonotal sides with a pair of thinner, truncate or slightly pointed teeth. Basal face of the propodeum with the pair of spines reaching the anterior third of the declivous face.

Petiolar sides medially with a pair of thin spines curved backwards.

Gaster shorter.

Sculpture. Body less punctate, more shining and with deeper and slightly larger foveae.

Colour. Black. Frontal carinae with one or two pairs of small, ferruginous, semitransparent spots. Lamellaceous border of the gaster yellow to ferruginous and semitransparent. Gaster with a pair of light yellow spots anteriorly. Tibiae and tarsomeres dark ferruginous.

Measurements (in mm) and indices: TL 6.74–8.02; HL 1.80–2.22; HW 2.28–2.68; EL 0.50–0.52; PW 1.88–2.20; PeW 0.85–0.96; PpW 0.76–0.90; HBaL 0.60–0.70; HBaW 0.14–0.18; CI 113.7–126.7; PI 113.0–121.3; PPeI 221.2–229.2; PPpI 239.0–247.4; HBaI 23.3–25.7.

G y n e (previously undescribed). - Differing from *inaequalis* in the following: head less broad and much more convex. Frontal carinae strongly converging anteriorly; their sides parallel, gently upturned and surpassing behind the eyes posteriorly. Vertexal angles obtuse and slightly diverging towards the ventral border of the eyes. Vertex simply convex or with a pair of median, minute denticles.

Mesosoma. Scapular angles reduced and not visible in full dorsal view. Humeral angles with a pair of spines longer and more acute. Pronotal crest narrow, superficially marked on

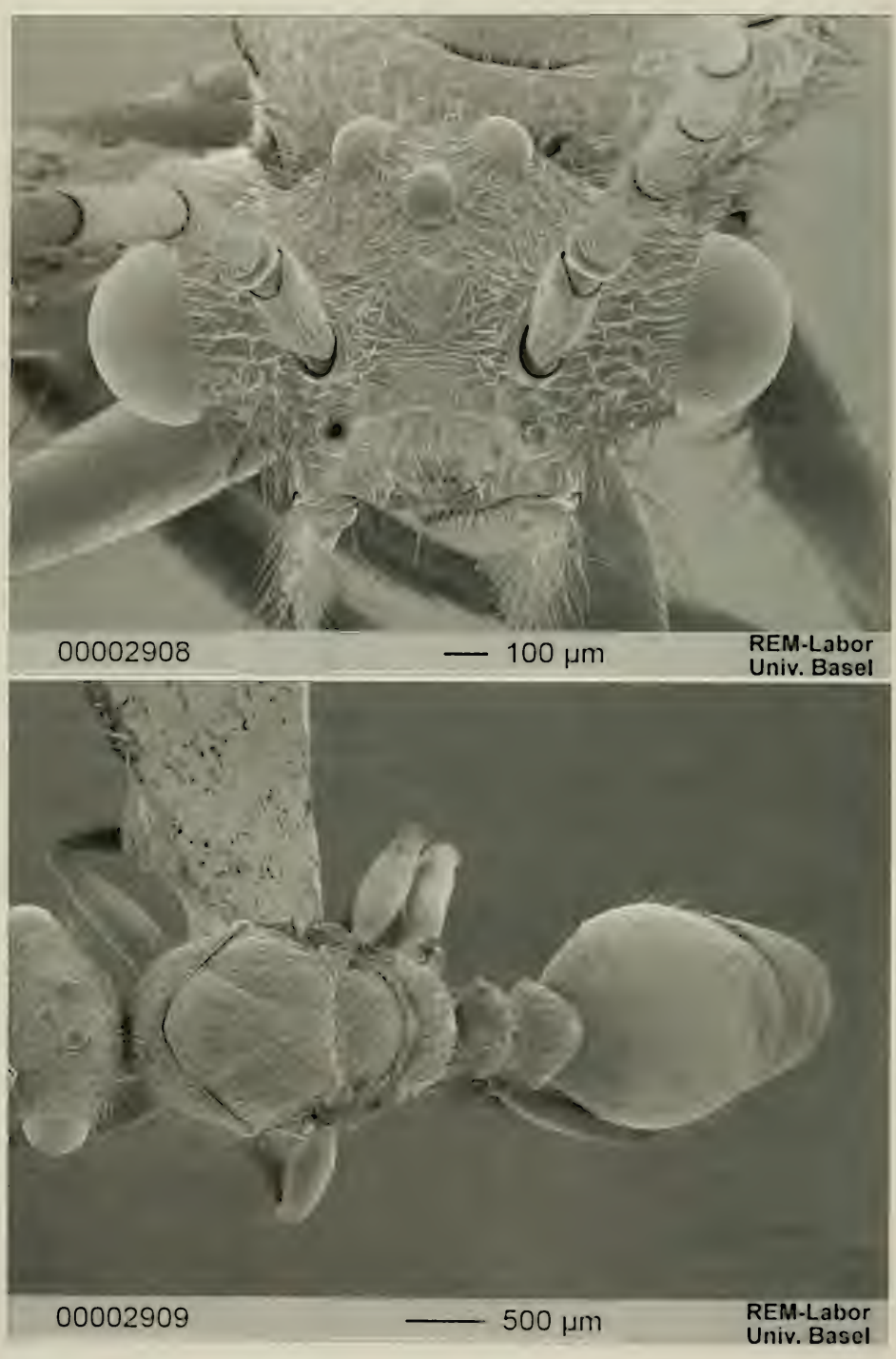


Fig. 96. *Cephalotes laminatus* (SMITH). Male from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

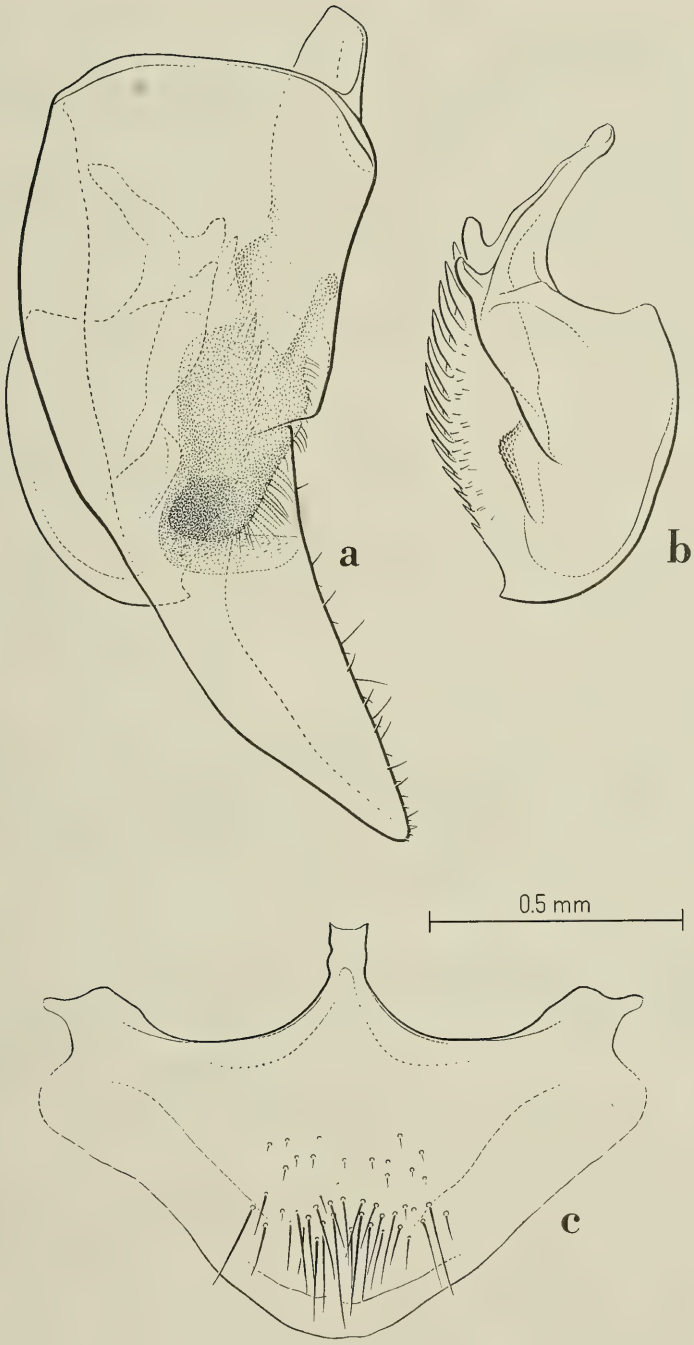


Fig. 97. *Cephalotes laminatus* (SMITH). Male from Manaus, Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

the sides and interrupted in the middle. Basal face of the propodeum anteriorly straight or weakly convex and followed by a pair of teeth pointed or round. Propodeal teeth directed backwards or slightly diverging.

Petiolar sides unarmed or with a pair of small median denticles. Postpetiole, laterally, with a pair of truncate lobes instead of spines.

Gaster with a pair of marginate anterior lobes.

Wings as in Fig. 95.

Sculpture. Body foveae deeper and slightly larger. Lower metapleurae with transversal, thin rugosities on the dorsal half.

Pilosity. Clubbed hairs on the mesosoma and on the first gastral tergite rare and absent on the pedicel.

Colour. Black. Frontal carinae with one or two pairs of ferrugineous and semitransparent spots. Gaster with two pairs of yellow spots, the first pair on the anterior third and the second one before the posterior border of the first tergite. Tibiae and tarsomeres dark-ferruginous.

Measurements (in mm) and indices: TL 12.00–13.02; HL 2.46–2.50; HW 2.64–2.76; EL 0.55–0.56; PW 2.56–2.60; PeW 1.08; PpW 1.28–1.44; HBaL 0.80–0.81; HBaW 0.20–0.22; CI 107.3–110.4; PI 103.1–106.1; PPeI 237.0–240.7; PPpI 180.5–200.0; HBaI 25.0–27.2.

M a l e (Fig. 96) (previously undescribed). - Head (eyes included) more than 1/3 broader than long. Vertex strongly protruding dorsally. Compound eyes broadly convex. Frontal carinae short and not reaching the median ocellus posteriorly. Frons flat. Clypeus dorsally convex; its anterior border with a pair of broad denticles. External face of the mandibles without carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards, without carinae. Mesonotal scutum convex in side view; median Mayrian furrow very superficial. Basal and declivous faces of the propodeum differentiate; basal face gently convex and sloping backwards; declivous face posteriorly marked by a pair of longitudinal, converging carinae.

Petiole with deeply concave anterior face; posterior face sloping posteriorly and flat. Petiolar sides convex. Postpetiolar sides with a pair of small denticles medially.

Gaster slightly broader than the mesosoma.

Genitalia and subgenital plate as in Fig. 97.

Wings as in the gyne.

Sculpture. Head dorsum minutely reticulate-punctate and with irregular rugosities and foveae, the rugosities thinner on the posterior half, irregular and transversal around the eyes; the foveae denser on the vertexal area. Clypeus strongly reticulate. Ventral part of the head reticulate, punctate and with irregular foveae. Pronotum, mesonotum, scutellum, pro- and mesopleurae minutely and superficially reticulate, punctate and covered with shallow, variably clumped foveae, the reticulation more impressed on the pronotum. Basal face of the propodeum and upper metapleurae punctate and with sparse and irregular longitudinal rugosities, the rugosities continuing on the declivous face but thinner. Lower metapleurae with longitudinal rugosities. Sides of the petiole and dorsum of the postpetiole superficially reticulate and with the sides covered with irregular foveae and short, thin, longitudinal rugosities. First gastral tergite reticulate and with superficial longitudinal rugosities. Remaining tergites and sternites superficially reticulate-punctate and slightly shining. Legs punctate, the punctures more impressed on the tarsi.

Pilosity. Body with light ferrugineous, flexuous, thin, pointed hairs dense on the head, on the mesosoma, on the pedicel, on the ventral face of the femora, and on the gaster. Legs with additional similar hairs but shorter and appressed.

Colour. Black with lighter gaster. Legs yellow.

Measurements (in mm) and indices: TL 6.58; HL 0.92; HW 1.28; EL 0.45; PW 1.08; PeW 0.66; PpW 0.73; HBaL 0.77; HBaW 0.11; CI 139.1; PI 118.5; PPeI 163.6; PPpI 147.9; HBaI 14.3.

Material examined. - **Brazil**: no further locality, 1 worker (lectotype) [OXUM]. Amazonas: no further locality, 2 workers, 1 soldier (probably belonging to the type series), H. W. Bates S. [MHNG, ZSMC]; Manaus, 3°09' S, 60°00' W, 13.IX.1987, 60 m, 2 workers, 1 soldier, 1 gyne, 1 male, P. S. Ward [INPA]; Res. Flor. A. Ducke, 2°55' S, 59°59' W, 21.II.1992, 1 worker, A. Adis et al. [INPA]; Manaus, 2F3, km 24, Fazenda Esteio, Florestal, 22.III.1983, day, 1 worker, A. Y. Harada [INPA]; Humaitá, Pto. Velho Rd. km 20, 10.IV.1975, 1 worker, V. P. da Silva [MZSP]. Pará: Belém, different days in VII, IX & X.1959, 59 workers, 10 soldiers, 1 gyne, N. Rosa [MZSP]; Belém, Inst. Agron. Norte, 06–19.IV.1963, 1 worker, 1 soldier, F. G. Werner [MCZC]; Serra Norte, Manganês, 9–18.IX.1985, 1 worker, 1 soldier, W. França [MPEG]; same locality, 5–9.IX.1983, 2 workers, M. P. Torres [MPEG]; Serra Norte, Serraria, 7–10.IX.83, 1 worker [MPEG]; Santarém Novo, Fazenda Jaburu, 7–9.I.1993, 1 worker, J. Dias [MPEG]; Marajó-Breves, Rio Caruacá, 3–6.VIII.1988, 1 worker, J. Dias [MPEG]; Carajás, VII-VIII.1985, 1 worker, C. R. F. Brandão & W. Benson [MZSP]. Rondônia: Vilhena, XI.1973, 1 worker, M. Alvarenga [MZSP]; same locality, 24.VII, 02.VIII.1983, 2 workers, A. Y. Harada [INPA, MZSP]. Acre: Cruzeiro do Sul, 11.III.1983, 3 workers, F. H. Caetano [MZSP]. Mato Grosso: Sinop, 55°37' W, 12°31' S, X.1974, 7 workers, M. Alvarenga [MZSP]; Vila Vera, X.1973, 15 workers, M. Alvarenga [MZSP].

Discussion. - The material available for the present study shows a good morphological uniformity for all the diagnostic characters. The workers from Rondônia, two workers from Manaus (P. S. Ward leg.) and some specimens from Pará differ systematically from the type and from other ones for having much more diverging propodeal spines.

Distribution: Brazil.

5.6.6. The *basalis* clade

A relatively large clade containing nine Recent and one fossil species. It is characterised by the following synapomorphies: (1) worker propodeum with a pair of spines shorter than the basal face, a trait secondarily lost among the more specialised species *inca* and *basalis*; (2) worker with incrassate fore femora, a character invariant within the clade and similar but probably not homologous to the condition characteristic of *Procryptocerus*, and, (3) soldier without vertexal denticles. In our reconstruction this character state results as a secondary loss of the clade which should have been re-gained among the most specialised species *basalis* and *cordiventris*.

Species included in the clade: *basalis*, *brevispineus*, *complanatus*, *cordiae*, *cordiventris*, *femoralis*, *inca*, *manni*, *mompox*, *ramiphilus*.

Cephalotes manni (Kempf) new combination

Fig. 98

Paracryptocerus manni Kempf, 1951: 228, figs. 127, 128. Worker, soldier. Original description. Type locality: Cachoeira Breu (Pará, Brazil). Type material: holotype and 1 paratype workers labelled "Est. Pará, Cachoeira Breu, X.1928, Sampaio" in MZSP, examined.

Zacryptocerus manni (Kempf), Brandão, 1991: 387. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *basalis* clade characterised: in the worker, by the vertexal angles broad and almost round, by the mid and hind basitarsi narrow and not compressed at the base and by three pairs of pronotal and three pairs of propodeal teeth; in the soldier, by the vertexal margin concave and by the frontal carinae anteriorly with a marginal row of clubbed hairs.

Worker (Fig. 98) (description of Kempf, 1951). - "Length 4.0 mm. Median head length 1.05 mm; Weber's length of thorax 1.22 mm. Black; the following ferruginous: tip of

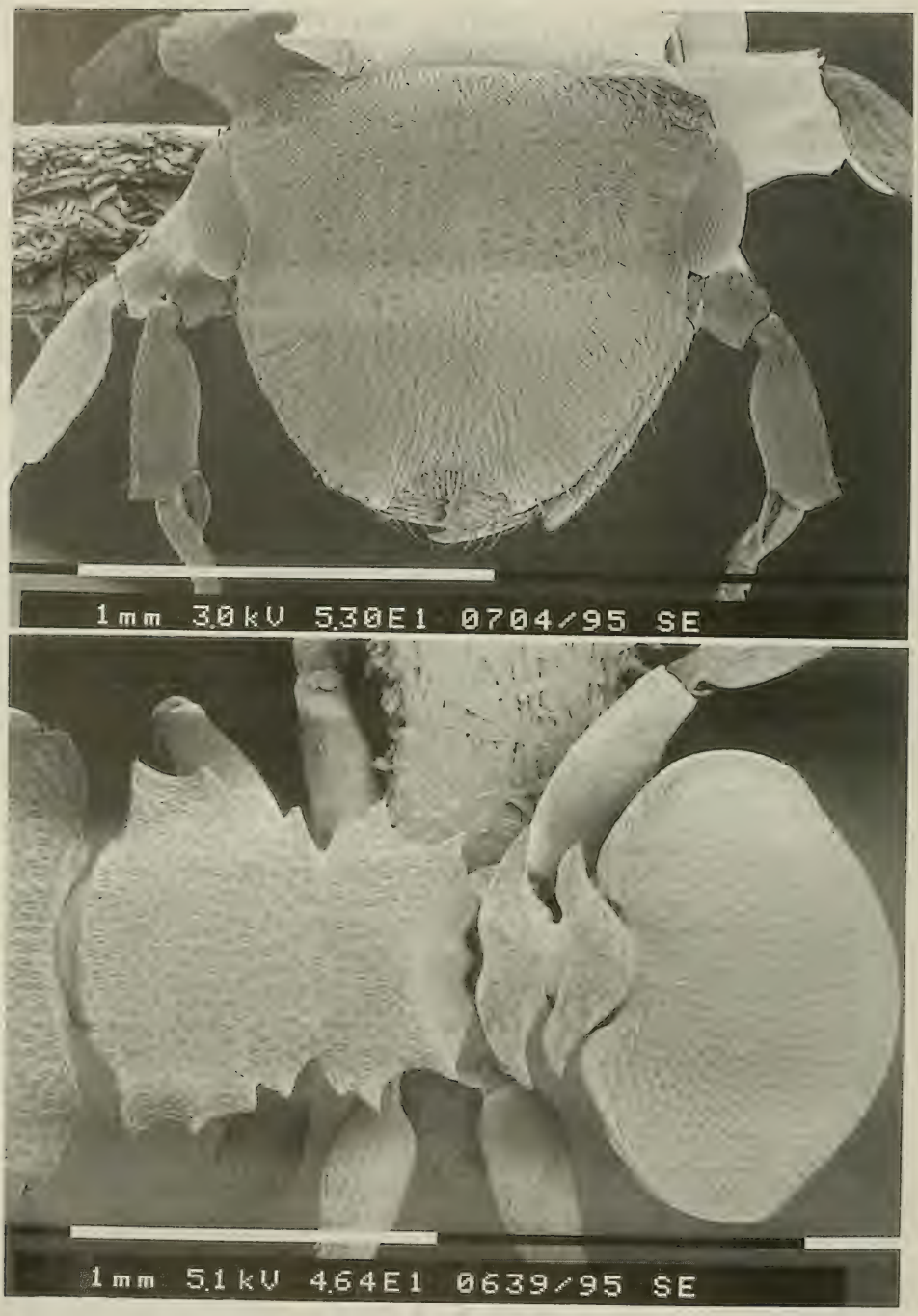


Fig. 98. *Cephalotes manni* (KEMPF). Worker from Kartabo, Guyana: head (top) and meso- and metasoma (bottom) in dorsal view.

mandibles, frontal carinae, tip of scape, first funicular segment, tip of femora, tibiae, fore tarsi, 2 – 4 middle and hind tarsi, anterolateral crest of gaster. Tip of thoracic and peduncular spines rufous brown.

Head subopaque. Mandibles finely reticulate-punctate and rugulose. Frontal carinae without crenulate border, beset with projecting setulae on the anterior half, the setulae arising from above. Posterior portion of frontal carinae slightly diverging caudad, and strongly sinuate, emarginate in front of, convex and upturned above, the eyes, a few erect setae above the eyes. Eyes prominent, their maximum diameter longer than 1/3 of median head length. Occipital corners obliquely subtruncate, the occipital border evenly concave. Cheeks strongly marginate beneath, very densely scaled. Upper surface of head scarcely convex, very finely and densely reticulate-punctate, sparsely covered with simple, appressed, flattened, silvery hairs, which became canaliculate and situated in more or less excavated grooves in front of the occipital border.

Thorax subopaque. Pronotum with a tridenticulate crest on each side. Mesonotum with an acute lateral tooth. Promesonotal and mesoepinotal sutures obsolete. Basal face of epinotum with a pair of small teeth near the anterior corner and a third tooth on the posterior corner, the posterior border of which is prolonged behind in a crest, delimiting the declivous face laterad and behind, as in *simillimus*. Upper surface of thorax finely reticulate-punctate, with scattered longitudinal grooves, each containing a decumbent, silvery canaliculate scale. Laterotergite of pronotum longitudinally striated. Sides of thorax finely reticulate with sparse, simple, appressed setae. Femora incrassated, somewhat compressed, angulate above at the half. Basitarsi slender, not conspicuously flattened and broadened at base.

Petiole subopaque, the anterior face truncate, with a strong lateral somewhat recurved spine. Postpetiole as long as petiole, with a slightly shorter, lateral spine, curved forward at base, slightly recurved at apex. Sculpture of both peduncular segments as on upper surface of thorax.

Gaster subopaque, oval. Greatly emarginate mesad in front, distinctly crested anterolaterad, the crest extending backward over more than half of the sides of the first gastral tergite, fading out shortly in front of the apical third. Upper surface of gaster finely reticulate-punctate, rather densely covered with mostly simple, silvery appressed scales, lying in shallow grooves. Erect pile confined to tergites 2 – 4 and the apical border of sternite I and the following sternites."

Measurements (in mm) and indices: TL 4.04–5.06; HL 1.00–1.24; HW 1.24–1.58; EL 0.40–0.42; PW 1.00–1.32; PeW 0.68–0.85; PpW 0.60–0.80; HBaL 0.32–0.41; HBaW 0.08–0.12; CI 121.1–127.4; PI 119.7–124.0; PPeI 144.4–155.3; PPpI 162.5–168.7; HBaI 23.5–29.3.

S o l d i e r (description of KEMPF, 1951). - "Length 6 mm. Median head length 1.41 mm. Weber's length of thorax 1.66 mm. Black; the following ferruginous: tip of mandibles, outer portion of frontal carinae, tip of femora, tibiae and tarsi. The first funicular segment and the tip of the last segment lighter.

Head subfulgid; subquadrate, anterior corners greatly rounded, posterior corners subrectangular. Mandibles angular, reticulate rugose. Frontal carinae extending to the occipital corner, upturned, crenulate, with a rim of projecting clubbed setulae. Upper surface of head slightly convex discad. Occipital border straight, crested, with a median depression. Occiput not truncate beneath the crest, confluent with the lower surface of the head. Eyes elongate, ovoid. A distinct carina extended from beneath the eye to the occipital corner. Upper surface of head finely reticulate, coarsely and rather densely foveolate, with a simple, decumbent, glittering hair in each foveola. Lower surface of head with the microsculpture partly obsolete, more fulgid, reticulate-foveolate.

Thorax subfulgid above. Pronotum greatly expanded; anterior border arcuate, shoulders obsolete, not set off, the sides greatly expanded, anterior corners acutely angulate, sides straight, converging towards the mesonotum, the posterior corners rounded, and slightly depressed. Pronotum with a transverse crest, flat, continuous with the mesonotum, in the same plane. Promesonotal suture vestigial. Sides of mesonotum with an obliquely truncate, lateral lobe, the posterior corner of which is slightly upturned. Mesoepinotal suture impressed laterad, obsolete discad. Basal face of epinotum with a basal rectangular tooth, and, following,

a larger similar plate-like tooth, and a broad, more or less rounded lobe on the posterior corner, the posterior, (internal), border of which is continuous with the emarginate posterior border of the basal face. Upper surface of thorax sculptured as on head, foveolae more crowded. Laterotergite vestigially longitudinally striated. Sides and declivous face subopaque, finely reticulate-punctate. Femora incrassated, somewhat compressed, indistinctly angulate above at the half.

Petiole and postpetiole as in worker, the spines shorter and stouter, and somewhat blunt at apex.

Gaster subopaque, elongate, broadest behind the half. First gastral tergite conspicuously emarginate anteriorly mesad, submarginate, nor crested, antero-laterad. Upper surface finely reticulate-punctate, with scattered, minute silvery, simple appressed hairs. Erect pilosity as in worker."

Measurements (in mm) and indices: TL 6.00; HL 1.40; HW 1.68; EL 0.42; PW 1.64; PeW 0.83; PpW 0.81; HBaL 0.36; HBaW 0.12; CI 120.0; PI 102.4; PPeI 197.6; PPpI 202.5; HBaI 23.5.

Material examined. - **Colombia**: Amazonas: Territory Witoto Aimeni Unomiai, 19.XII.1973, 2 workers, J. Desplats [MNHN]; La Chorrera, 30 km downhill Río Igara Paraná, 26.II.1974, 1 worker, J. Desplats [MNHN].

Guyana: Kartabo, Jul.-Aug. 1920, 7 workers, 1 soldier, (2 workers and 1 soldier erroneously labelled as paratypes by Kempf), W. M. Wheeler [MCZC].

Brazil: Amazonas: High Falls, Rio Tarumã, 30.VIII.1962, 1 worker, W. L. Brown [MCZC]. Pará: Left side of the Tucuruí, 14.III.1979, 1 worker, R. B. Neto [MPEG]; Cachoeira Breu, X.1928, 2 workers (holotype and paratype), Sampaio [MZSP]; Porto das Trombetas, 01.VIII.1992, 2 workers, J. D. Majer [CPCC]. Rondônia: Vilhena, BR 364, Terreno do João, 02.VIII.1983, 1 worker, A. Y. Harada [INPA].

Peru: Madre de Dios: Avispas, 400 m, 01–15.X.1962, 1 worker, Peña [MCZC].

Discussion. - *C. manni* is the smallest species of the *basalis* clade. It is somehow intermediate between the species of the *laminatus* and of the *basalis* clade. The worker and the soldier of *manni* are similar to the species of the *laminatus* clade for the first tarsomere of the mid and hind legs not flat; in addition, the worker shares with the members of the *laminatus* clade the superficial, elongate foveae on the body and the ventral part of the head finely reticulate. *Manni*, however, exhibits all three synapomorphies of the *basalis* clade resulting from our analysis (worker with incrassate and incavate fore femora, basal and declivous faces of the propodeum separate by a short spine and secondary loss of the vertexal spines in the soldier) and has no vertexal lamella (the presence of which is synapomorphic for the *laminatus* clade).

Distribution: Colombia, Guyana, Brazil, Peru.

† *Cephalotes brevispineus* de Andrade new species

Figs. 14 A, 99

Type material: Holotype worker (unique) in the Dominican amber sample H 10–105 in the GOPC.

Derivatio nominis: from the Latin *brevis* (= short) and *spineus* (= bearing spines) referred to the morphology of the propodeal spines.

Diagnosis. - A member of the *basalis* clade characterised by the broad vertexal lamella of the worker.

Worker (Fig. 99). - Head slightly broader than long. Vertexal angles with a round, broad lamella. Vertex without denticles. Vertexal margin concave. Mandibles laterally angulate.

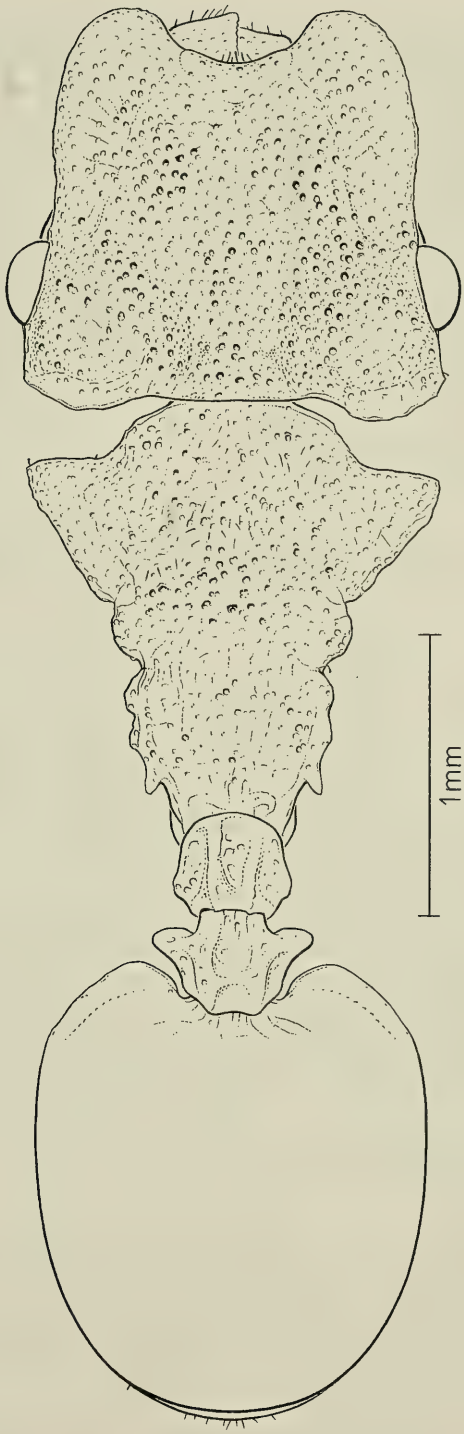


Fig. 99. *Cephalotes brevispineus* DE ANDRADE from Dominican Amber. Worker in dorsal view. Appendages omitted.

Mesosoma. Scapular angles absent. Anterior pronotal border strongly protruding anteriorly. Pronotal sides with a broad, long, continuous, triangular lamella narrowing posteriorly. Promesonotal suture absent. Sides of the mesonotum armed with a pair of broad, short, round teeth. Propodeal suture superficially impressed. Propodeum with differentiate basal and declivous faces; basal face with two pairs of short, broad, irregular denticles followed by a pair of pointed teeth; declivous face converging posteriorly.

Petiolar lateral expansions lost in the unique specimen. Anterior petiolar face truncate. Postpetiolar sides anteriorly with a broad, round tooth.

Gaster suboval and with a pair of anterolateral lamellae.

Hind femora angulate. Mid and hind basitarsi flat.

Sculpture. Head, mesosoma and peduncular segments minutely reticulate and with small, superficial foveae variably clumped; the reticulation less impressed on the propodeum and on the pedicel; the foveae sparser and more superficial on the pedicel. Pleurae, gastral tergites and legs reticulate, the reticulation less impressed on the centre of the first gastral sternite.

Pilosity. Each fovea with a minute, appressed hair. Border of the vertexal angles, of the pronotal lamellae with rare, short clubbed hairs. First gastral sternite with long, rare, suberect, pointed hairs.

Colour. Black. Frontal carinae, vertexal angles, border of the pronotal lamellae and gastral lamellae ferrugineous.

Measurements (in mm) and indices: TL 5.08; HL 1.20; HW 1.47; EL 0.30; PW 1.47; PeW 0.42; PpW 0.60; HBaL (left) 0.40; HBaL (right) 0.50; HBaW (left) 0.17; HBaW (right) 0.15; CI 122.5; PI 100.0; PPeI 350.0; PPpI 240.0; HBaI 42.5 (left); HBaI (right) 30.0.

Material examined. - **Dominican amber**: 1 worker (holotype) in the GOPC (reference number: H 10–105).

Discussion. - *C. brevispineus* resembles in body shape the Recent *manni* with which it shares the basal face of the propodeum with three denticles differing in size and the ventral face of the head finely and superficially reticulate. On the other hand, *C. brevispineus* can be easily differentiated from *manni* by the shape of the vertexal angles and of the pronotal lamellae.

The large workers of *manni* resemble much more *brevispineus* in the propodeal and pronotal morphology than the smaller ones.

For the cladistic analysis the femora of this species have been tentatively coded as inflate (char. 57). This is much more a deduction than an objective description of what is visible in this unique, poorly preserved specimen. The inflate femora, however, are an important synapomorphy of the *basalis* clade with the members of which *brevispineus* shows great similarities in the general habitus.

Distribution: Dominican amber.

Cephalotes cordiae (STITZ) new combination

Figs. 100, 101

Cryptocerus cordiae STITZ, 1913: 207, fig. 1. Worker and soldier. Original description. Type locality: Alto Acre (Brazil). Type material: one syntype worker labelled "Brasilien, Alto Acre", in NHMW (examined) and one syntype soldier also in NHMW (KEMPF, 1951: 199).

Paracryptocerus cordiae (STITZ), EMERY, 1922: 307. First combination in *Paracryptocerus*.

Paracryptocerus cordiae (STITZ), KEMPF, 1951: 199, figs. 132, 140. Gyne.

Zacryptocerus cordiae (STITZ), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *basalis* clade characterised in the worker and soldier by the propodeum with only a pair of spines, and, in all castes, by the HBaI $\geq$ 53 (the sole known gyne has HBaI = 57.5, the highest of the clade).

W o r k e r (description of KEMPF, 1951). - "Length 6.4 mm. Median head length 1.45 mm; Weber's length of thorax 2.07 mm. Black; the following fuscous ferruginous; apex of mandibles, anterior corner of frontal carinae, three apical tarsal segments. Tip of last funicular segment orange-brown.

Head subopaque, subquadrate. Mandibles very finely reticulate-punctate, not rugulose. - Sides of head not sinuate, not upturned above the eyes. Forontal carinae greatly curved mesad in front, prolonged behind the scrobe, fading out above the eyes. Occipital corner obtusely angulate, more or less rounded. Occipital border almost straight, scarcely emarginate mesad, not crested nor marginate laterad. Upper surface conspicuously convex, finely reticulate-punctate, more sparsely and somewhat vestigially foveolate, each foveola containing a small, usually simple, bright, shiny and appressed scale. Cheeks weakly to indistinctly carinate below, rather densely covered with large, silvery, appressed, canaliculate scales. Lower surface of head more fulgid, with sparser scales.

Thorax subopaque. Sides of lateral pronotal plates strongly converging caudad, their lateral border crested, the anterior corner subspinose, the posterior corner rounded. Promesonotal suture obsolete mesad. Mesonotum with a lateral, apically rounded, lobe-like tooth. Mesoepinotal suture impressed. Basal face of epinotum without a lateral tooth, sides moderately arcuate, immarginate, the posterior corner with a longer, somewhat divergent and upturned spine, shorter than the length of the basal face. Promesonotum in profile, conspicuously convex. Posterior border of basal face submarginate. Declivous face longer than basal face, the sides marginate. Dorsum of thorax finely reticulate-punctate, without distinctly impressed foveolae, scales sparse, short and simple. Sides of thorax and declivous face finely reticulate. Tibiae prismatic.

Petiole and postpetiole subequal in width, subopaque, without a median longitudinal carinule above. Spines of petiole upturned and slightly recurved.

Gaster subopaque, elongate, finely reticulate-punctate. First gastral tergite scarcely emarginate mesad, narrowly crested antero-laterad, with simple, minute scattered, appressed scales. Erect hairs confined to the following tergites and sternites."

Measurements (in mm) and indices: TL 5.32–5.86; HL 1.36–1.48; HW 1.64–1.76; EL 0.37–0.44; PW 1.52–1.68; PeW 1.16; PpW 1.04–1.08; HBaL 0.56–0.60; HBaW 0.31–0.32; CI 118.9–120.6; PI 104.8–107.9; PPeI 131.0–144.8; PPpI 140.7–161.5; HBaI 53.3–55.3.

S o l d i e r (Fig. 100) (description of KEMPF, 1951). - "Length 7.3 mm. Median head length 1.78 mm; Weber's length of thorax 2.19 mm. Black.

Head subfulgid; subquadrate. Mandibles smooth, subfulgid, sparsely punctate. Frontal carinae greatly curved mesad in front, scarcely raised, continued behind the scrobe as a faint carina, fading out above the eyes, not reaching the rounded occipital corner. Clypeus obliquely inclined, not perpendicular to the conspicuously convex upper surface of head. Vertex without a pair of median teeth. Occiput distinctly truncate, immarginate above. Cheeks submarginate with a vestigial carina below the eyes reaching back to the occipital corner. Upper surface of head smooth, very finely punctate, sparsely covered with very small, vestigial foveolae, not containing a distinctly visible hair. Hair more apparent on lower surface of head.

Thorax subfulgid to subopaque. Pronotum greatly expanded laterad, the anterior border conspicuously arcuate, the anterior corner angulate and subspinose, the lateral border not crested, the sides converging caudad. Promesonotum, in profile, greatly convex, pronotum without a distinct transverse crest or margination. Promesonotal suture vestigial. Mesonotum with a strong, apically rounded, lateral, lobe-like tooth. Mesoepinotal suture impressed, scarcely arcuate caudad. Basal face of epinotum rounded anteriorly the sides immarginate, subparallel, without a tooth, the posterior corner with a strong, rather short, slightly divergent and slightly upturned spine, the basal face being somewhat impressed above, in front of the base of each spine. Posterior border of basal face scarcely emarginate, but marginate. Dorsum of thorax and laterotergite of pronotum microscopically punctate, with sparse, more or less obsolete foveolae. Mesopleura and metapleura very finely, superficially reticulate with a few scattered scale-like hairs. Declivous face smooth, fulgid, superficially and very finely reticulate.

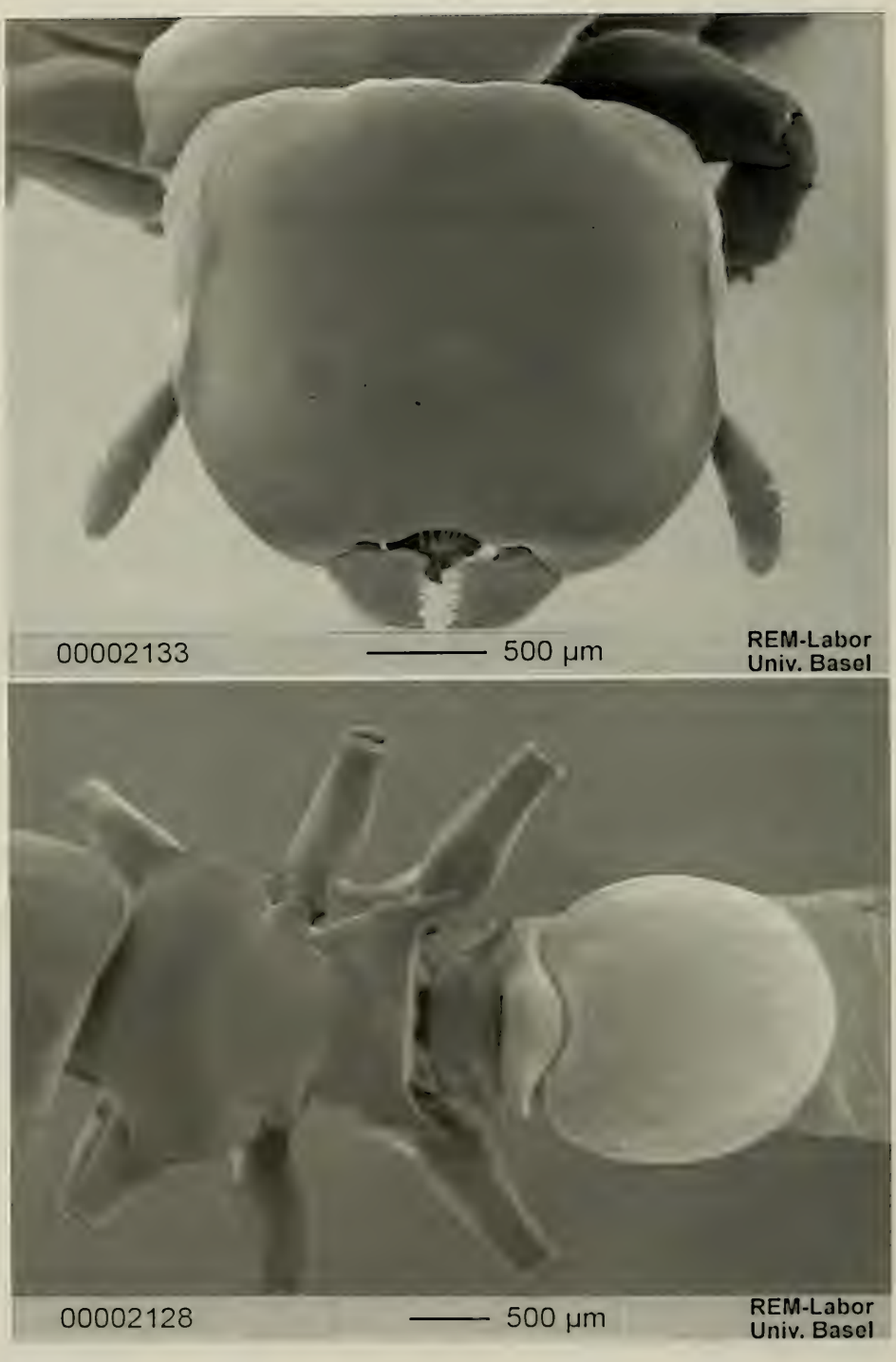


Fig. 100. *Cephalotes cordiae* (STITZ). Soldier from Puerto Maldonado, Peru: head (top) and meso- and metasoma (bottom) in dorsal view.

Petiole with smooth anterior truncate face, immarginate above mesad, submarginate laterad. The upper face rather vestigially scaled and foveolate. The spines greatly upturned and recurved. Postpetiole as wide as petiole, the spines not upturned, rather stout, blunt at apex.

Gaster subopaque, finely reticulate-punctate, broadly subcordiform. The first gastral tergite scarcely emarginate anteriorly mesad, not distinctly crested, but marginate antero-laterad, with rather dense, scattered, minute appressed shiny setulae. Sternites subfulgid, shallowly and finely reticulate, more sparsely scaled. Erect sparse setae on the following tergites and the sternites of the gaster."

Measurements (in mm) and indices: TL 6.88–7.52; HL 1.68–1.84; HW 1.98–2.12; EL 0.43–0.44; PW 1.88–2.00; PeW 1.12–1.20; PpW 1.08–1.16; HBaL 0.67; HBaW 0.36; CI 115.2–117.8; PI 105.3–106.0; PPeI 166.7–167.8; PPpI 172.4–174.1; HBaI 53.7.

G y n e (description of KEMPF, 1951). - "Length 10 mm. Median head length 2.12 mm; interocular width 2.17 mm; Weber's length of thorax 3.07 mm. Black; the anterior corner of the frontal carinae, the tibiae, tarsi, sides and apical border of the gastral sclerites with rufous hues.

Head, as in soldier, fulgid, finely and shallowly punctate. Median head length subequal to interocular width. Mandibles fulgid, finely and sparsely punctured, with a projecting anglle above, near the base. Frontal carinae not upturned, not prolonged above beyond the eyes.- Upper surface of head greatly convex, with very sparse, larger punctures. Cheeks immarginate above and below; no carinule beneath the eyes. Ocelli light and colorless. Occiput truncate, immarginate above and below. Occipital corners bluntly rounded. Lower surface of head sparsely and more coarsely punctate-foveolate.

Thorax fulgid, its maximum length subequal to the length of the first gastral tergite. Pronotum above with a transverse blunt keel, not interrupted mesad. Sides immarginate, with a stout, short, conical scapular tooth, pointing obliquely foreward. Part of pronotum in front of the keel subvertical. Basal face of epinotum very short, transverse, its posterior border emarginate and submarginate, having a stout conical tooth on each posterior corner. Declivous face perpendicular, much longer than the basal face. Upper mesopleura greatly convex, lower mesopleura with a tooth. Upper surface of thorax very finely punctate, very sparsely and vestigially foveolate. Sides and eclivous face finely and shallowly reticulate. Femora incrassated, somewhat compressed, angulate above. Tibiae twice as broad as thick. Mid and hind basitarsi greatly broadened and flattened proximad, narrower and less compressed distad, less than twice as long as broad.

Petiole with a stout conical tooth on each side. The anterior face obliquely truncate, marginate above, twice as long as the dorsal face. Postpetiole with a stout conical tooth on each side, its dorsal face greatly convex. Both peduncular segments fulgid and smooth, the microsculpture vestigial.

Gaster elongate oval, sides moderately convex, scarcely emarginate anteriorly, the anterior corners not producted, immarginate. Subfulgid, finely but distinctly reticulate, and sparsely and more or less vestigially foveolate.

Erect pile on mandibles, and apical segments of gaster; minute decumbent setulae on legs and the first gastral tergites and sternites."

Measurements (in mm) and indices: TL 10.00; HL 2.04; HW 2.24; EL 0.55; PW 2.08; PeW 1.24; PpW 1.32; HBaL 0.80; HBaW 0.46; CI 109.8; PI 107.7; PPeI 167.7; PPpI 157.6; HBaI 57.5.

M a l e (Fig. 101) (previously undescribed). - Head, eyes included, about 1/3 broader than long; vertexal margin straight in the middle and diverging laterally into two convex angles. Vertex and ocelli slightly protuberant. Eyes convex and placed in the middle of the sides of the head. Frontal carinae not raised and shortly diverging backwards. Frons gently convex and separate from the clypeus by a superficial furrow. Clypeus convex, its anterior border almost truncate. Mandibles short and without carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with marked scapular angles and broadening backwards. Mesonotum convex; median Mayrian carina weakly impressed. Scutellum convex,

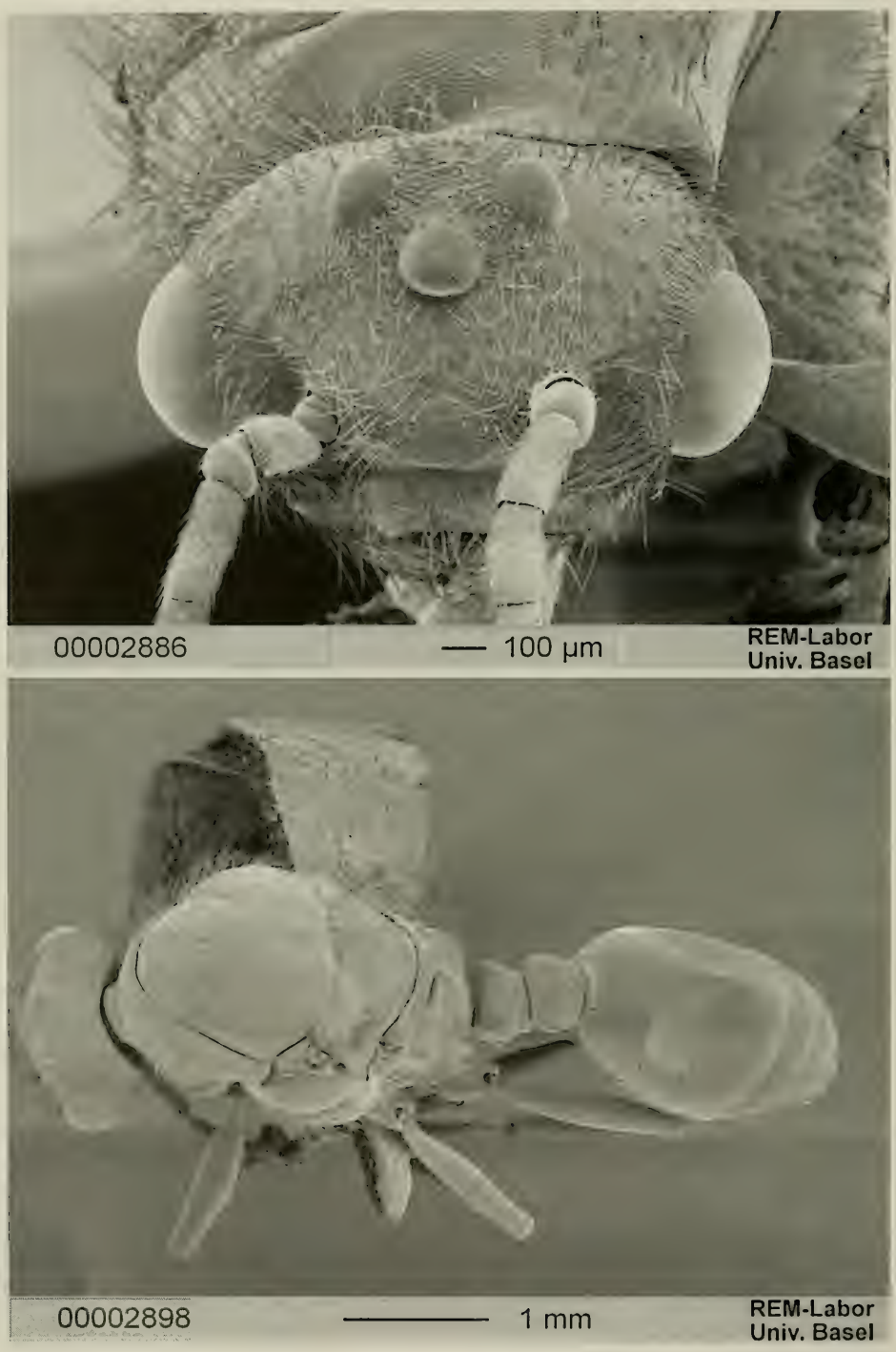


Fig. 101. *Cephalotes cordiae* (STITZ). Male from Puerto Maldonado, Peru: head (top) and meso- and metasoma (bottom) in dorsal view.

its sides converging posteriorly. Propodeum with differentiate basal and declivous faces; basal face with the sides posteriorly converging and angulate; declivous face converging posteriorly and laterally marginate.

Petiole with the anterior face truncate and with the posterior face gently sloping backwards; petiolar sides convex. Postpetiole convex dorsally; postpetiolar sides gently convex, the sole specimen available has the left side with a small medial denticle and the right side simply convex.

Gaster narrower than the mesosoma.

Sculpture. Head and pronotum reticulate and with small, sparse, very superficial foveae, denser on the vertexal angles. Mesonotum and scutellum reticulate, with deeper and larger foveae than on the vertexal angles. Propodeum reticulate and with slightly longitudinal rugosities. Mesopleurae anteriorly reticulate and with dense, superficial, small foveae, this sculpture rare on the posterior half. Posterior half of the mesopleurae and metapleurae weakly shining and with longitudinal rugosities more impressed on the lower metapleurae. Propleurae, declivous face of the propodeum, pedicel, gaster and legs reticulate, the reticulation less impressed on the legs and on the gastric sternites.

Pilosity. Head, mesosoma and pedicel covered by long, suberect hairs, sparser on the pedicel; similar hairs but sparse on the posterior border of the gastral tergites, of the sternites and on the legs. Gaster and legs with appressed, thin, short hairs.

Colour. Head, mesosoma and pedicel dark brown, femora and gaster lighter. Remaining parts of the legs yellowish and light brown.

Note: the colour of this male may not represent the adult coloration since the sole available specimen is likely to be a freshly emerged one; the genitals have been not dissected to avoid possible damaging; the wing venation is also almost indistinguishable.

Measurements (in mm) and indices: TL 6.48; HL 0.96; HW 1.24; EL 0.49; PW 1.52; PeW 0.63; PpW 0.64; HBaL 0.72; HBaW 0.14; CI 129.2; PI 81.6; PPeI 241.3; PPpI 237.5; HBaI 19.4.

Material examined. - **Brazil**: Acre: Alto Acre, 1 worker (syntype) [NHMW].

Peru: Madre de Dios: Cuzco Amazônico, 15 km NE of Puerto Maldonado, July 1989, 1 worker, 4 soldiers, 1 male, on *Cordia alliodora*, S. P. Cover & J. E. Tobin [MCZC].

Bolivia: Beni: Rurrenabaque, 1921–1922, 4 workers, 3 soldiers, W. M. Mann [MCZC, MZSP]; C. Esperanza, March, 1921–1922, 1 gyne, W. M. Mann, Mulford Biol. Exp. [USNM].

Discussion. - The workers of *C. cordiae* share with *ramiphilus*, its closest relative, the high HBaI (≥ 47 in both species as compared with < 43 in the other species of the clade except *femoralis*). The worker and the soldier of *cordiae* can be easily distinguished from those of *ramiphilus* for the presence of only one pair of spines between the basal and declivous face of the propodeum and for the obtuse anterior border of the pronotal lamellae. The gyne of *cordiae* differs from that of *ramiphilus* for the sculpture, more superficial. According to Stitz (1913) the type series has been also collected on *Cordia*.

Distribution: Peru, Bolivia, Brazil.

Cephalotes ramiphilus (Forel) new combination

Figs. 102, 103, 104

Cryptocerus complanatus ramiphilus Forel, 1904: Worker and soldier. Original description. Type locality: Bom Fim do Juruá (Amazonas, Brazil). Type material: lectotype worker in MHNG (Kempf, 1951: 198); a specimen detached in the *ramiphilus* drawer in the MHNG without corresponding pin and labels of any kind could represent the lectotype designated by Kempf (1951: 158) of which we find no traces either in MHNG or in MZSP. This specimen had been re-mounted and labelled "*C. ramiphilus* (Forel), lectotype of Kempf 1951?".

Syntypes examined: 1 worker and 1 soldier labelled "Bom Fim Jurua, Nov. 1900, in perforated twigs of *Platymiscium ulei* Harms. *Cr. complanatus* Guérin r. *ramiphilus* Forel, type, Amazonas (Ule)" [MHNG].

Paracryptocerus complanatus ramiphilus (FOREL), KEMPF, 1951: 196, figs. 130, 135. Worker and soldier. First combination in *Paracryptocerus*.

Paracryptocerus ramiphilus (FOREL), KEMPF, 1967: 363.

Zacryptocerus ramiphilus (FOREL), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *basalis* clade differing from its sister species *cordiae*, by the propodeum with two or three pairs of teeth (instead of one) in the worker, and simply convex (instead of with one diverging spine), in the soldier, and, in the gyne, by the body less shining and with more impressed foveae.

W o r k e r (Fig. 102) (description of KEMPF, 1951). - "Length 5.4 mm. Median head length 1.27 mm; Weber's length of thorax 1.51 mm. Black; the following fuscous ferruginous: apex of mandibles, apical three tarsal segments. Tip of last funicular segment yellowish.

Head subopaque, subquadrate. Mandibles finely reticulate-punctate and rugulose. Sides of head very little sinuate, not upturned above the eye. Frontal carinae prolonged behind the scrobe as a distinct carina, not reaching the occipital corner. Occipital corners rounded, occipital border straight, scarcely emarginate mesad, sharply carinate laterad. Upper surface of head moderately convex, finely reticulate-punctate, sparsely covered with very shallow elongate grooves, each containing a large, usually canaliculate, appressed, silvery, scale-like hair. Cheeks strongly carinate below, densely covered with silvery, appressed scales. Lower surface of head more fulgid, scales sparser.

Thorax subopaque. Sides of lateral pronotal plates more or less subparallel, anterior and posterior corners rounded. Promesonotal suture obsolete. Mesonotum with a strong lateral spine. Mesoepinotal suture obsolete. Basal face of epinotum with a broad, plate-like, triangular tooth on each side, having on its anterior border a minute, rather blunt, denticule, and a posterior, rather short, slender, acuminate spine, projecting obliquely backwards, about as long as half the length of the basal face. Pronotum convex in profile. Mesoepinotum flat longitudinally, slightly convex transversely. Posterior border of basal face of epinotum submarginate. Sides of declivous face carinate. Dorsum of thorax finely reticulate-punctate, with sparse, squamiferous foveolae, scales conspicuous, appressed, silvery and canaliculate. Sides of thorax and declivous face very finely and distantly longitudinally striated, and very finely reticulate. Tibiae prismatic. Petiole and postpetiole subopaque, petiolar spines upturned and somewhat recurved. Both segments without a dorsal median longitudinal carinule.

Gaster subopaque, elongate, cordiform. First gastral tergite conspicuously emarginate anteriorly mead, broadly crested antero-laterad, sculptured as upper surface of the thorax, foveolae vestigial, scales more slender, and simple. Erect hair on the following tergites and the sternites."

Measurements (in mm) and indices: TL 5.16–6.68; HL 1.24–1.56; HW 1.56–1.92; EL 0.40–0.48; PW 1.38–1.76; PeW 1.00–1.40; PpW 0.88–1.20; HBaL 0.51–0.52; HBaW 0.24–0.27; CI 116.2–125.8; PI 109.1–113.0; PPeI 125.7–147.1; PPpI 146.6–165.9; HBaI 47.0–51.9.

S o l d i e r (Fig. 103) (description of KEMPF, 1951). - "Length 7 mm. Median head length 1.87 mm; Weber's length of thorax 2.09 mm. Black.

Head fulgid, subquadrate; rounded anteriorly and posteriorly. Mandibles finely reticulate-rugose. Frontal carinae scarcely raised, continued behind the scrobes as a distinct carina, above the eyes, fading out before reaching the occipital corner. Upper surface of head moderately convex, vertex without teeth. Occiput distinctly truncate, submarginate above mesad, marginate laterad. Cheeks submarginate beneath, the lower border continuing behind below the eyes as a distinct carina, reaching the occipital corner. Upper surface of head smooth, sparsely and rather finely foveolate, the foveolae containing a minute yet visible hair. Lower surface of head more sparsely foveolate, the foveolae with a more conspicuous hair.

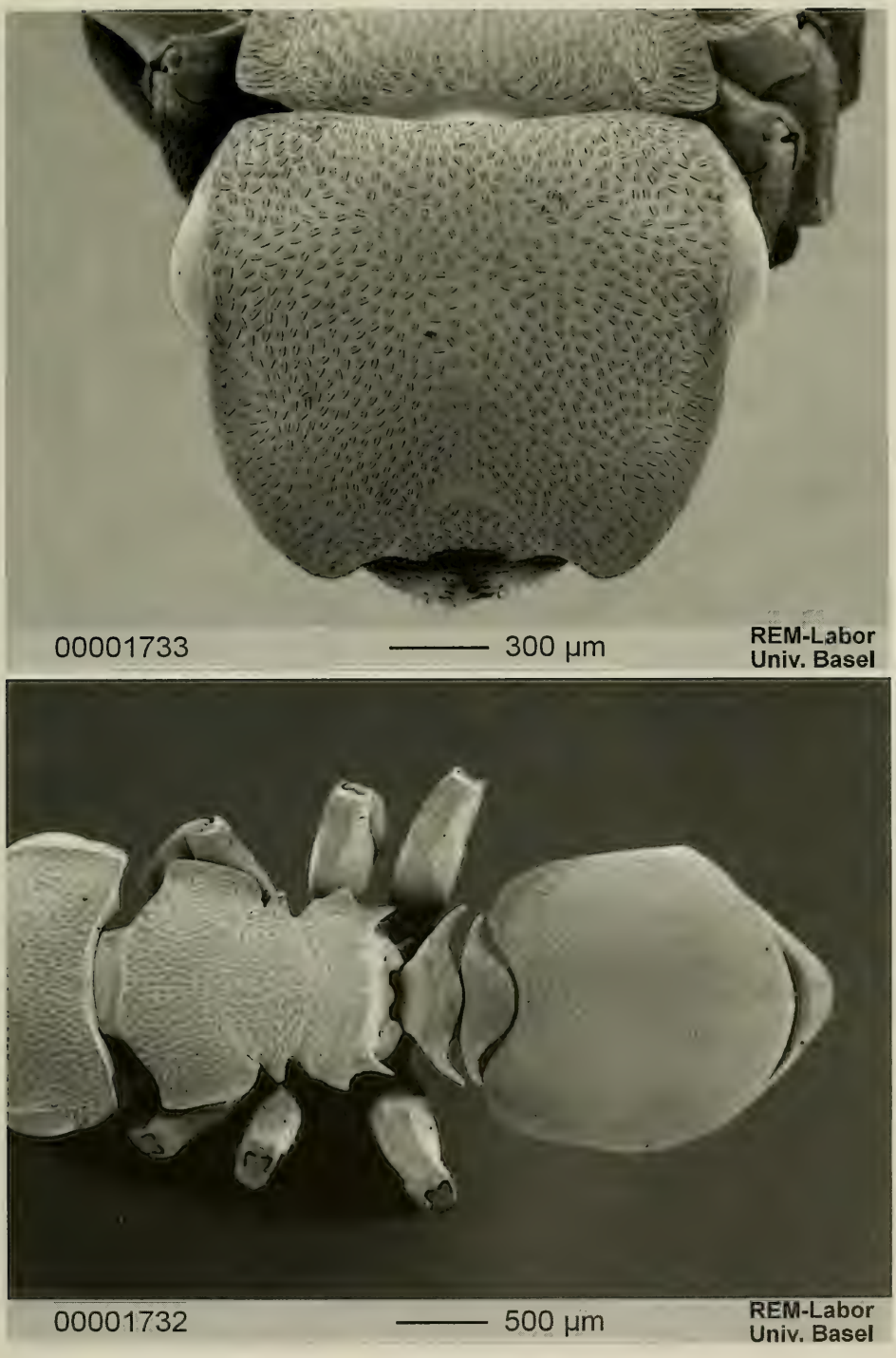


Fig. 102. *Cephalotes ramiphilus* (FOREL). Worker from Itacoatiara, Amazonas, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

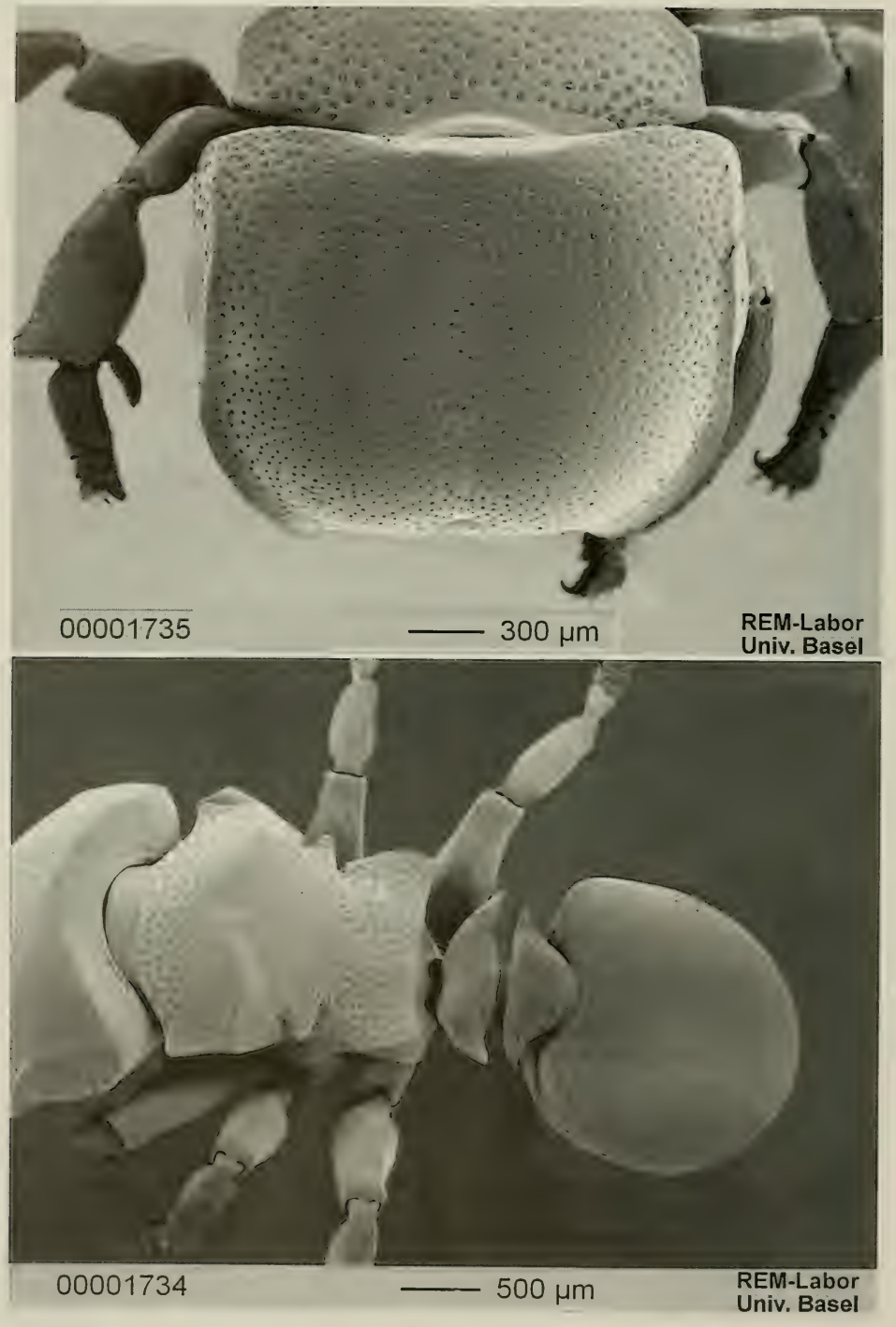


Fig. 103. *Cephalotes ramiphilus* (FOREL). Soldier from Ixiamas, Bolivia: head (top) and meso- and metasoma (bottom) in dorsal view.

Thorax subfulgid. Pronotum expanded laterad, the anterior border conspicuously arcuate, the anterior corner angulate, the sides parallel and crested onto the transverse pronotal crest, then abruptly bent mesad, towards the mesonotum. Transverse pronotal crest distinct laterad, somewhat obsolescent mesally. Promesonotal suture vestigial. Mesonotum with a strong apically rounded lateral tooth. Mesoepinotal suture impressed, scarcely arcuate. Basal face of epinotum without a lateral spine, sides arcuate and crested, the posterior corner with a small, not divergent, tooth, the posterior border sharply marginate. Declivous face smooth, slightly excavate, superficially and very finely reticulate. Promesonotum finely punctate, basal face of epinotum and sides of thorax very finely, shallowly reticulate-punctate. Dorsum of thorax, laterotergite of pronotum sparsely foveolate, with rather large, golden, always visible scales within the foveolae. Scales very conspicuous on basal face of epinotum. Upper face of tibiae and apical half of upper face of femora rather densely scaled.

Petiole with smooth anterior truncate face, marginate above. The upper face scaled and foveolate. The spines not greatly upturned, stouter than in worker. Postpetiole similarly sculptured, the spines not upturned.

Gaster subopaque, finely reticulate-punctate, elongate, subcordiform. The first gastral tergite moderately emarginate anteriorly mesad, narrowly crested laterad, with scattered, minute, glistening, appressed setulae. Sternites subfulgid, shallowly and very finely reticulate, more sparsely scaled. Erect, sparse setae on the apical third of the gaster."

Measurements (in mm) and indices: TL 7.00–8.08; HL 1.76–2.00; HW 2.08–2.28; EL 0.48–0.52; PW 1.88–2.24; PeW 1.08–1.44; PpW 1.10–1.32; HBaL 0.52–0.60; HBaW 0.28–0.32; CI 114.0–118.1; PI 101.8–110.6; PPeI 147.2–174.1; PPpI 160.6–170.9; HBaI 51.7–53.8.

G y n e (Fig. 104) (previously undescribed). - Head convex, without disc. Frontal carinae converging anteriorly and straight posteriorly up to the end of the eyes. Vertexal angles rounded and marginate. Vertex marked by a faint, straight carina. Mandibles with a lateral carina.

Mesosoma. Humeral angles broad and obtuse. Pronotal carina poorly marked on the middle and faintly on the sides. Mesonotum and scutellum flat in side view. Lower mesopleurae with a denticle. Sides of the basal face of the propodeum convex anteriorly, converging posteriorly and with a broad, pointed tooth; declivous face converging posteriorly.

Petiole distinctly differentiated in anterior and posterior faces; anterior face oblique; the posterior face declivous posteriorly. Petiolar sides with a pair of pointed spines directed backwards. Postpetiole broadly convex, with the spines arising from its anterior border and directed laterally.

Gaster marginate anteriorly.

Legs. Fore coxae tumuliform anteriorly. Mid and hind femora marked by an angle. Mid and hind basitarsi flat and broad at the base.

Sculpture. Head minutely reticulate-punctate and covered by small foveae with the interspace between them larger than their maximum diameter. Frontal carinae with shallower foveae than those on the head. Vertexal area, ventral part of the head, mesosoma and pedicel with round foveae larger and deeper than those on the head dorsum, sparser on the ventral face of the head and on the occipital area behind the head dorsum, and contiguous on the basal face of the propodeum and on the dorsal part of the mesopleurae. Declivous face of the propodeum, posterior half of the ventral part of the mesopleura, metapleurae, legs and gaster reticulate-punctate and slightly shining, with faint longitudinal rugulations on metapleurae.

Pilosity. Each fovea bearing a thin, appressed hair; mandibles, and legs with rare, slightly clavate, suberect hairs. Second and remaining tergites and sternites with two types of hairs: rare, long pointed hairs, and thick, erect, truncated hairs, shorter than the pointed one.

Colour. Black. Last funicular joints ferruginous.

Measurements (in mm) and indices (based on one specimen from Leticia, Colombia): TL 9.20; HL 1.84; HW 2.00; EL 0.52; PW 1.96; PeW 1.10; PpW 1.22; HBaL 0.64; HBaW 0.29; CI 108.7; PI 102.0; PPeI 178.2; PPpI 160.6; HBaI 45.3.

M a t e r i a l e x a m i n e d . - No locality, 1 worker, 2 soldiers, 1954, W. M. Mann [USNM]. **Colombia:** A m a z o n a s : 35 km above Leticia, 70–90 m, 05.IX.1973, 5 workers, 1 gyne, M. L. Corn [MZSP].

Ecuador: N a p o : Campanococha, 17.XII.1984, 1 worker, L. Torres [MZSP].

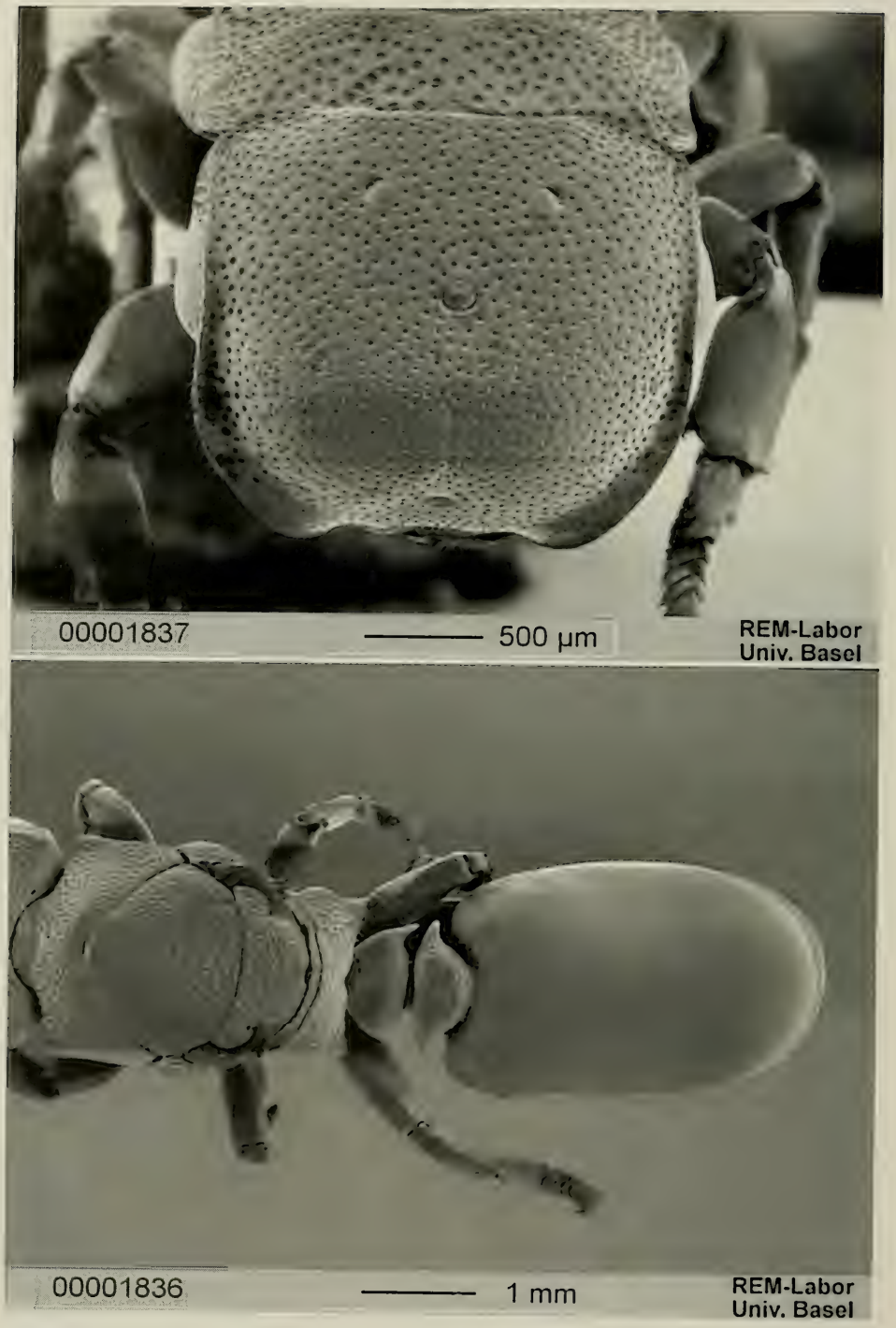


Fig. 104. *Cephalotes ramiphilus* (Forel). Gyne from Leticia (Amazonas), Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

Peru: H u á n u c o : Pachitea (= Pachitea river?), 1 worker [MCSN].

Brazil: A m a z o n a s : no further locality, 1 worker, 1 soldier, H. W. BATES [ZSMC]. Bom Fim do Juruá, Nov. 1900, in perforated twigs of *Platymiscium ulei* HARMS, 1 worker, 1 soldier (syntypes), E. ULE [MHNG]; Itacoatiara, 3 workers, 2 soldiers, MANN & BAKER [MCZC, USNM].

Bolivia: L a P a z : Ixiamas, Dec. 1921–1922, 1 soldier, W. M. MANN, Mulford Biol. Exp. [USNM].

D i s c u s s i o n . - *C. ramiphilus* and *cordiae* are the two species in the *basalis* clade sharing round vertexal angles and high HBaI. Both species are represented by few specimens in the collections; nonetheless only the male of *ramiphilus* is still unknown. *C. ramiphilus* and *cordiae* are restricted to northern South America, with *ramiphilus* occurring more in the north and *cordiae* more in the south. The two species appear to occur parapatrically in the NW part of Brazil.

D i s t r i b u t i o n : Colombia, Ecuador, Brazil, Peru, Bolivia.

Cephalotes complanatus (GUÉRIN)

Figs. 105, 106, 107

Cryptocerus complanatus GUÉRIN, 1845: 284. Worker. Original description. Type locality: Cayenne, French Guyana. Type material presumably lost, not in the ZSMC. A specimen (but not a type) labelled *complanatus* from Magdalena, Colombia in the Guérin collection at the ZSMC is actually *C. femoralis*.

Cryptocerus angulatus SMITH, 1858: 189, pl. 12, fig. 4. Soldier. Original description. Type locality: Tunantins (Brazil). Type material: soldier in the Museum of the Department of Entomology, University of Oxford (KEMPF: 1959: 97), not available for the present study, and a soldier labelled "Tunantins" and "57 125" in the BMNH, examined. Synonymy by EMERY, 1922: 307.

Cryptocerus multispinus var. *amazonensis* FOREL, 1911 b: 261. Worker. Original description. Type locality: Amazon. Type material: two syntype workers labelled "Amazonas, H. W. Bates S.", one in MHNG and one in ZSMC, examined. Synonymy by KEMPF, 1951: 193.

Paracryptocerus complanatus (GUÉRIN), KEMPF, 1951: 193, fig. 131, 136. Worker (and soldier?). First combination in *Paracryptocerus*.

Paracryptocerus complanatus (GUÉRIN), KEMPF, 1959: 97, fig. 2. Soldier.

Zacryptocerus complanatus (GUÉRIN), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

Cephalotes complanatus (GUERIN), BARONI URBANI, 1998: 320, fig. 1. Worker and soldier, caste polymorphism. First combination in *Cephalotes*.

D i a g n o s i s . - A member of the *basalis* clade characterised, in the worker, by the following combination of characters: frontal carinae weakly upturned over the eyes and ending in a triangular angle, in the soldier, by the frontal carinae upturned before the eyes up to the vertexal angles, and, in the gyne, by the first gastral tergite with a pair of orange spots not covered by hairs.

W o r k e r (description of KEMPF, 1951). - "Length 6.9 mm. Median head length 1.68 mm; Weber's length of thorax 2,04 mm. Black; the following fuscous ferruginous: apex of mandibles, three apical tarsal segments. Tips of last funicular segment yellowish-brown.

Head subopaque, subquadrate. Mandibles finely reticulate-punctate, finely longitudinally rugulose. Sides of head very little sinuate, somewhat converging anteriorly, frontal carinae curved mesad, forming a blunt, small tooth in front of the eye, prolonged behind as a distinct carina, reaching the occipital corner, very scarcely upturned above the eye. Occipital corner forming a distinct angle. Occipital border emarginate mesally, sharply crested laterad. Upper surface of head very little convex, finely reticulate-punctate, more sparsely covered with shallow, oval grooves, each containing a conspicuous, usually canaliculate, silvery, appressed scale.

Cheeks strongly carinate below, densely covered with large, canaliculate, silvery scales. Lower surface of head more fulgid, with sparser scales.

Thorax subopaque. Sides of lateral pronotal plates somewhat converging behind, anterior corner angulate, posterior corner rounded. Promesonotal suture obsolete. Mesonotum with a strong lateral spine. Mesoepinotal suture vestigial. Basal face of epinotum with a large, broad triangular, plate-like tooth on each side and a posterior rather short, slender, acuminate spine, projecting obliquely backward, much shorter than the length of the basal face. Promesonotum, in profile, somewhat convex. Posterior border of basal face of epinotum submarginate. Sides of declivous face carinate. Dorsum of thorax finely reticulate-punctate, with sparse, squamiferous foveolae, the scales being appressed and canaliculate. Laterotergite of pronotum longitudinally striated. Declivous face very finely, superficially reticulate. Tibiae prismatic.

Petiole and postpetiole subopaque, with a vestigial longitudinal medial carinule above, beginning behind the anterior border on the postpetiole. Spines of petiole upturned and slightly recurved.

Gaster subopaque, elongate, cordiform, shallowly emarginate anteriorly mesad; with an anterolateral foliaceous border. Sculpture as on dorsum of thorax, foveolae only vestigial, scales slender, simple. Erect hair confined to the terminal tergites and the sternites."

Measurements (in mm) and indices: TL 4.44–7.88; HL 1.12–1.92; HW 1.36–2.28; EL 0.38–0.53; PW 1.28–2.16; PeW 0.88–1.60; PpW 0.80–1.36; HBaL 0.45–0.76; HBaW 0.19–0.32; CI 121.4–135.0; PI 105.5–114.9; PPeI 130.0–146.8; PPpI 139.1–160.0; HBaI 40.0–42.2.

S o l d i e r (Fig. 105). - Head strongly convex, without disc. Frontal carinae broad anteriorly, slightly converging and upturned before the beginning of the eyes and ending in the vertexal angles. Vertexal angles obtuse. Vertex with a pair of median, small denticles connected each other by a faint carina. Mandibles with a thick, lateral carina.

Mesosoma. Humeral angles with a broad lateral lamella, its anterior border making a straight angle with the sides and converging posteriorly. Pronotal carina thick, strongly marked and broadly interrupted in the middle by a superficial notch. Promesonotal and propodeal sutures impressed. Mesonotum with a broad, round, protruding tooth. Propodeum clearly differentiated in basal and declivous faces. Basal face narrow anteriorly, strongly diverging posteriorly to a pair of broad, round expansions and followed by a pair of subround teeth.

Petiole with distinctly differentiated anterior and posterior faces. Anterior face truncate and separated from the posterior one by a superficial carina; posterior face sloping backwards. Petiolar spines as long as the petiolar length; their base almost as broad as the sides of the petiole, curved back- and upwards. Postpetiole with anterior and posterior faces; anterior face truncate, high and separate from the posterior one by a carina shortly interrupted in the middle. Postpetiolar spines arising from the anterior face of the postpetiole, ending on the middle of the postpetiolar sides, thick and directed laterally.

Gaster oval, with a broad lamella reaching the stigma posteriorly.

Legs. Fore coxae tumuliform anteriorly. Fore femora broad, not angulate. Outer face of the mid and hind femora with a pair of denticles on the middle. Mid and hind basitarsi flat; their base twice broader than the apex.

Sculpture. Head minutely and superficially reticulate-punctate, covered by faint, small, foveae smaller than their interspaces. Mesosoma with the same type of sculpture as the head dorsum, but with larger and denser foveae on the sides of the pronotum, on the propodeum and on the propleurae. Pedicel, lower meso- and metapleurae, distal part of the outer face of the femora, outer face of the tibiae and anterolateral third of the first gastral tergite with dense, oval foveae. Declivous face of the propodeum, upper part of the meso- and metapleurae, anterior face of the pedicel, legs, and first gastral sternite reticulate-punctate, almost shining, with minute, superficial foveae on the sternite. Remaining part of the first gastral tergite superficially reticulate-punctate and with small, superficial foveae.

Pilosity. Each fovea bears a thick, appressed, hair of thickness proportional to the size of the fovea. Legs with rare, appressed, short and thin hairs. Border of the gastral segments with

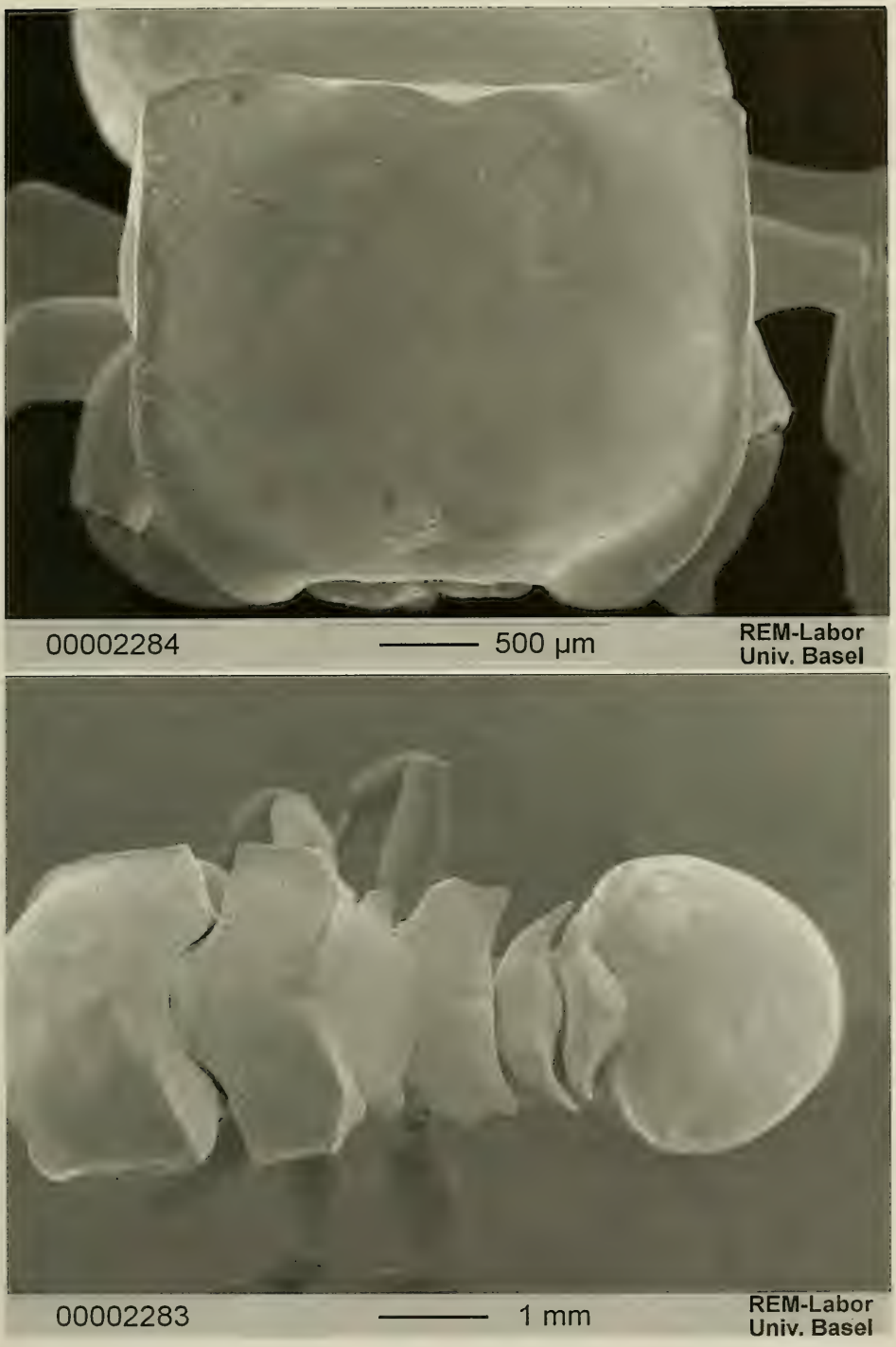
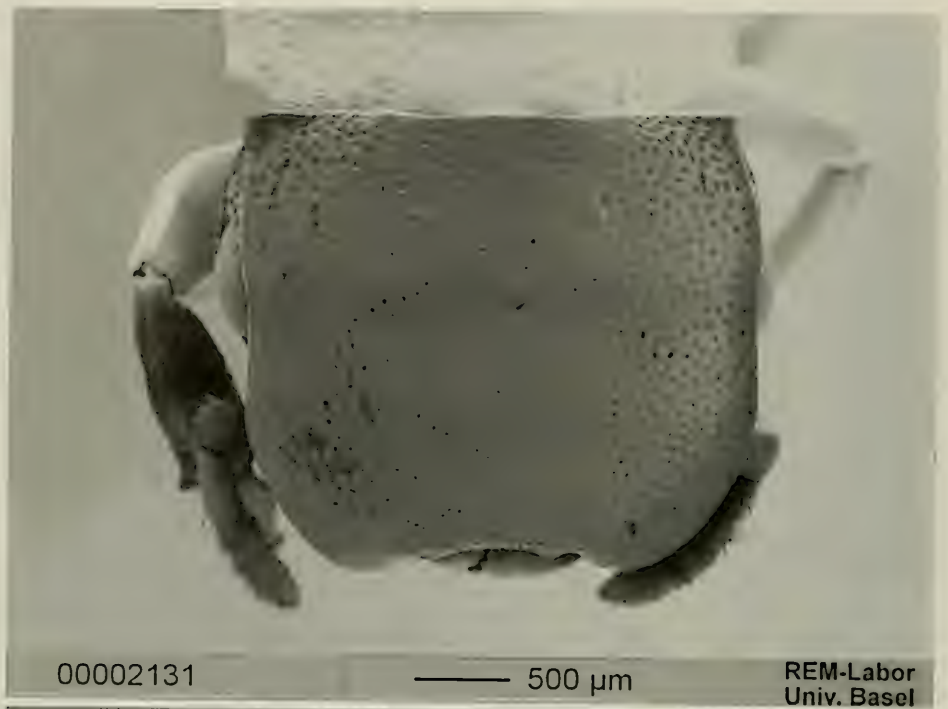


Fig. 105. *Cephalotes complanatus* (GUÉRIN). Soldier from Tefé (Amazonas), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.



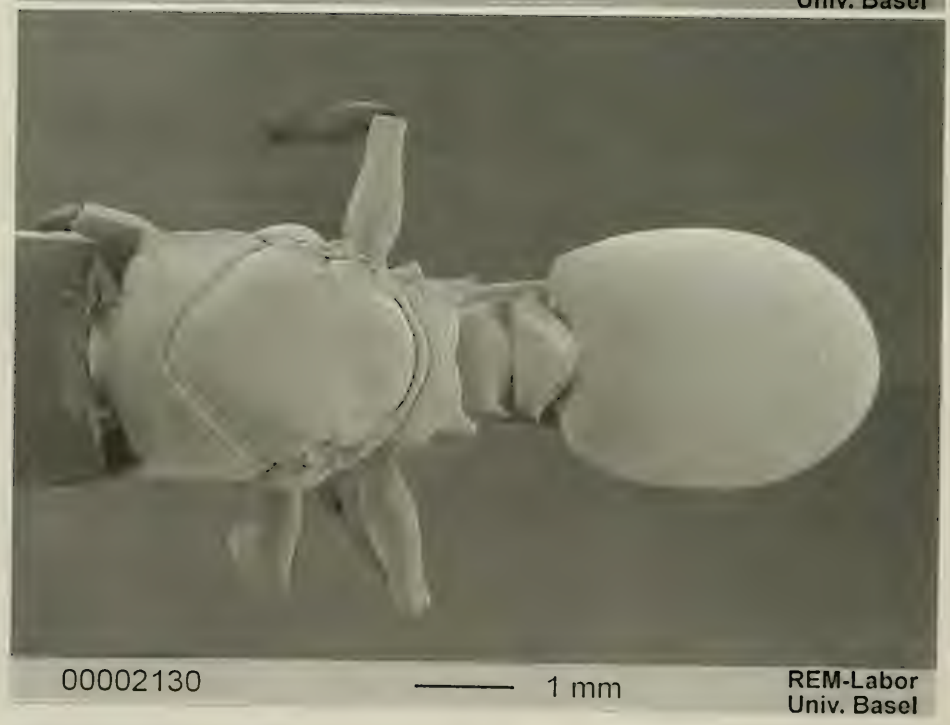


Fig. 106. *Cephalotes complanatus* (GUÉRIN). Gyne from Paramaribo, Surinam: head (top) and meso- and metasoma (bottom) in dorsal view.

long, slightly clavate hairs; similar hairs but more clavate on the legs. Border of the sternites with rare, long, pointed hairs.

Colour. Black almost shining. Tip of the last funicular joints orange.

Measurements (in mm) and indices: TL 9.04–10.04; HL 2.32–2.60; HW 2.76–2.96; EL 0.56–0.64; PW 2.60–2.88; PeW 1.60–1.92; PpW 1.40–1.72; HBaL 0.80–0.84; HBaW 0.32–0.36; CI –113.8–119.0; PI 102.4–106.1; PPeI 150.0–162.51; PPpI 167.4–185.7; HBaI 40.0–45.0.

G y n e (Fig. 106) (previously undescribed). - Head as in the soldier, but less convex, with the frontal carinae less broad and less upturned over the eyes. Vertexal angles more pointed. Ocelli far from the vertexal margin.

Mesosoma gently convex in profile. Pronotal sides angulate only. Pronotal carina superficially marked on the sides. Mesonotum flat in side view. Lower mesopleurae with a lateral tooth. Sides of the basal face of the propodeum with two pairs of teeth, the first pair broad and subtriangular, the second pair with parallel, not diverging, external sides, longer and more pointed than the first one. Declivous face of the propodeum with posteriorly converging sides.

Petiole with distinctly differentiate anterior and posterior faces; anterior face oblique truncate; posterior face sloping backwards. Petiolar sides with pointed, lateral spines slightly directed up- and backwards. Postpetiole convex; its anterior face higher than the petiolar dorsum; posterior face of the postpetiole not clearly separate from the anterior one by a "V" shaped carina; postpetiolar spines broad, short, pointed and directed laterally.

Gaster anterolaterally with protruding lobes and with a margin not reaching the stigma backwards.

Legs. As in the soldier.

Wings as in Fig. 107.

Sculpture. Head minutely and superficially punctate, covered by superficial, small, variably clumped foveae. Ventral face of the head superficially with large, sparse foveae. Mesosoma with the same type of sculpture as the head dorsum, but with larger and denser foveae on the sides of the pronotum, on the propodeum, on the propleurae and on the lower mesopleurae. Posterior face of the petiole and of the postpetiole with dense, oval foveae; similar sculpture but with foveae smaller on the distal part of the outer face of the femora and on the outer face of the tibiae. Upper mesopleurae with dense, small foveae. Declivous face of the propodeum, anterior face of the pedicel, upper metapleurae, first sternite and femora minutely and superficially reticulate-punctate, almost shining; this same type of sculpture but more impressed and opaque on the lower metapleurae and on the remaining parts of the legs. First gastral tergite minutely and superficially punctate and shining.

Pilosity. Each fovea bears a thick, appressed, hair of thickness proportional to the size of the fovea. Legs and gaster with appressed, short, thin hairs, denser on the gaster. Border of the gastral segments with long, slightly clavate hairs; similar hairs but shorter on the first sternite. Legs with short, sparse, clavate hairs. Border of the sternites with rare, long, pointed hairs.

Colour. Black shining. First gastral tergite with a pair of orange spots on the anterolateral third.

Measurements (in mm) and indices: TL 11.84–12.48; HL 2.48–2.52; HW 2.78–2.80; EL 0.56–0.60; PW 2.64–2.68; PeW 1.36–1.52; PpW 1.48–1.64; HBaL 0.90–0.96; HBaW 0.37–0.38; CI 110.3–112.9; PI 104.5–105.3; PPeI 176.3–194.1; PPpI 163.4–178.4; HBaI 39.6–42.1.

M a t e r i a l e x a m i n e d . - **French Guyana:** Cayenne, 1 worker, JELSKI [MHNG]. **Surinam**: Meerzorg, 08.III.1961, cacao grove, 1 worker, E. O. WILSON [MCZC]. P a r a m a r i b o : Paramaribo, 02.IX.1958, 1 gyne, on *Erythrina lauca*, P. H. V. DOESBURG [MZSP].

Brazil: A m a z o n a s : no further locality, 2 workers (syntypes of *amazonensis* FOREL), H. W. BATES S [MHNG, ZSMC]; Tefé, I.1962, 2 workers, 12 soldiers, R. CARVALHO [MCZC, MZSP]; "Tocandins" (prob. = Tocantins), 1 soldier (syntype of *angulatus* SMITH)

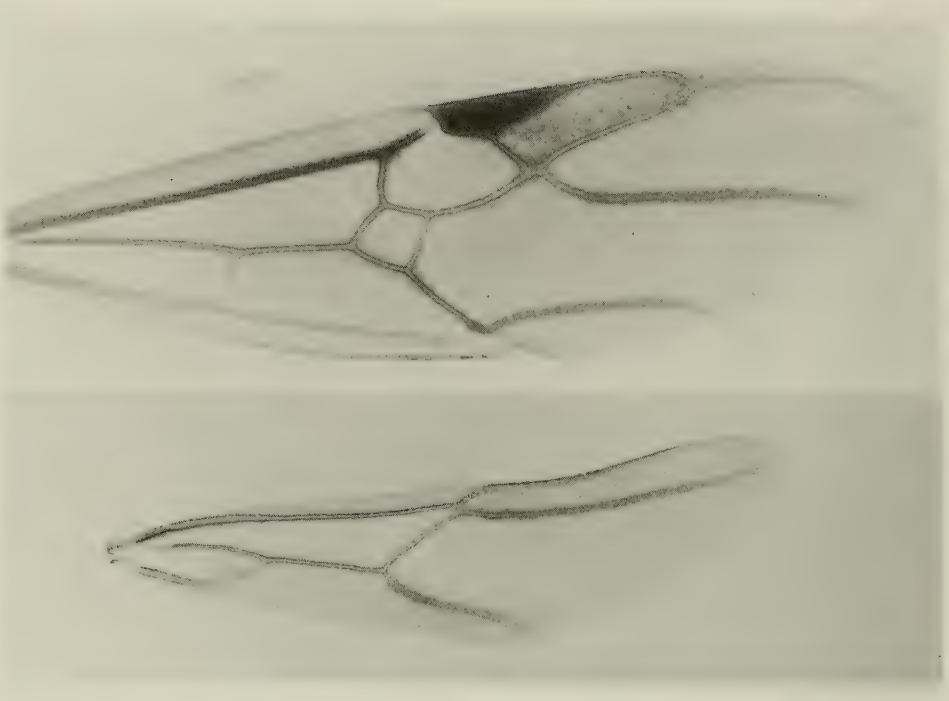


Fig. 107. *Cephalotes complanatus* (GUÉRIN). Gyne from Paramaribo, Surinam fore and hind wings.

[BMNH]. Pará: no further locality, 6 workers [MHNG, MCSN]; Primavera, Quatipuru, 26–30.XI.1992, 2 workers, J. DIAS [MPEG]; Serra Cipó Pitanga, baixo Rio Xingú, 3.XI.1983, 1 worker, B. MASCARENHAS [MPEG]; Tucuruí, Rio Arapari, 4.IV.1984, 1 soldier, T. PIMENTEL [MPEG]. Rondônia: Rio Madeira, Abunã, 1 worker, MANN & BAKER [USNM]. Mato Grosso: Utiariti, 325 m, Rio Papagaio, Jul. 1961, 4 workers, K. LENKO [MZSP]; Sinop, 55°37' W, 12°31' S, X.1974, 2 workers, M. ALVARENGA [MZSP].

Peru: Cuzco: Vilcanota, 1 soldier [MCSN]; Quincemil, IX.1962, 750 m, 1 worker, L. PEÑA [MCZC].

Bolivia: Beni: Cavinas, 1921–22, 1 worker, W. M. MANN [MCZC]. Santa Cruz: Sara, Nueva Moka, I. 1963, 1 gyne, A. MARTINEZ [MZSP].

Discussion. - The workers of *C. complanatus* from Mato Grosso differ from those of the other localities for the frontal carinae reduced to a thin margin over and behind the eyes and for the vertexal angles, obtuse. Small soldiers, in general, differ from the large ones by having the foveae denser and more impressed, and for the body more opaque.

KEMPF (1972) records *complanatus* from Colombia but no material from this country has been seen by us. FERNÁNDEZ et al. (1996) equally report this species from Colombia without further locality.

Distribution: French Guyana, Surinam, Brazil, Peru, Bolivia, Colombia.

Cephalotes cordiventris (SANTSCHI) new combination and new status
Figs. 108, 109, 110

Cryptocerus multispinus (EMERY) FOREL, 1899: 49. Worker and soldier, nec gyne. Pl. 3, figs. 9 and 10, nec fig. 11. Misidentification.

Cryptocerus multispinus var. *cordiventris* SANTSCHI, 1931 a: 274. Worker and soldier. Original description. Type locality: Canal Zone (Panama). Type material: 8 workers and 10 soldiers labelled "Panama, Canal Zone, Bierig, 1930" in NHMB (examined). Synonymy with *multispinus* by KEMPF, 1951: 204.

Paracryptocerus sp., CORNABY, 1974: 61.

D i a g n o s i s . - A member of the *basalis* clade differing from its sister species *mompox* by the absence of striation on the posterior face of the femora.

W o r k e r (Fig. 108). - Differing from *mompox* essentially in sculpture and little in morphology: small workers of *cordiventris* possess the pronotal lamellae less broad and converging posteriorly into a gently notched border, the propodeum less broad and the HBaI greater.

Sculpture. The reticulation and the foveae on the mesosoma are less dense than in *mompox*. Declivous face of the propodeum and legs minutely and superficially reticulate instead of longitudinally rugose.

Measurements (in mm) and indices: TL 6.32–7.44; HL 1.56–1.80; HW 1.88–2.28; EL 0.52–0.60; PW 1.78–2.24; PeW 1.20–1.48; PpW 1.12–1.28; HBaL 0.76–0.94; HBaW 0.27–0.32; CI 120.5–126.7; PI 101.9–105.9; PPeI 145.7–151.3; PPpI 158.9–175.0; HBaI 34.0–35.5.

S o l d i e r (Fig. 109). - Head subquadrate, convex and without disc. Vertexal angles obtuse. Vertex with a pair of small median teeth or simply a pair of swellings. Frontal carinae broad anteriorly, converging in front of the eyes and superficially marked behind the eyes. Mandibles broad, their sides with an impressed, round, carinate protuberance. Eyes almost flat.

Mesosoma. Anterior pronotal border convex. Pronotal sides with a pair of broad lamellae, pointed anteriorly, straight or gently convex medially and strongly converging posteriorly. Pronotal carina thick, raised and interrupted medially by an impression. Promesonotal suture impressed. Mesonotal sides with a pair of broad spines with pointed or round tip. Propodeal suture deeply impressed. Propodeum with differentiate basal and declivous faces; basal face either straight anteriorly or gently diverging over the whole sides into a pair of broad, large, pointed or round teeth. These teeth are followed by a concavity and by another, larger pair of teeth with round tip; sides of the declivous face converging posteriorly.

Petiole. Anterior face truncate; posterior face sloping backwards and with a superficial, median, transversal carina. Petiolar sides diverging posteriorly and with a pair of broad, long, pointed spines curved upwards. Dorsum of the postpetiole gently convex. Postpetiolar spines thick, pointed and arising from the anterior side of the postpetiole.

Gaster round, slightly longer than the mesosoma; anterolateral border of the first gastral tergite with a lamella not surpassing the first gastral stigma posteriorly.

Legs. Fore coxae tumuliform anteriorly. Fore femora as broad as or slightly narrower than the hind ones. Mid and hind femora angulate medially; mid and hind basitarsi laterally compressed and with broad base.

Sculpture. Head, mesosoma and pedicel minutely punctate and covered by small, superficial foveae smaller than their interspaces, larger and denser on the lateral part of the propodeal dorsum, on the petiole and on the postpetiolar spines. Ventral face of the head and propleurae minutely punctate and with the same sculpture as on the propodeal sides or with broader and deeper foveae in some specimens only. Lower meso- and metapleurae, outer face of the distal part of the femora, tibiae and anterolateral fourth of the first gastral tergite with dense, oval foveae. Declivous face of the propodeum, remaining parts of the pleurae and of the legs minutely reticulate-punctate. First gastral tergite with minute, superficial reticulation and foveae in small specimens; the same sculpture but less impressed and very shining in large specimens. First gastral sternite reticulate on the sides and shining in the middle.

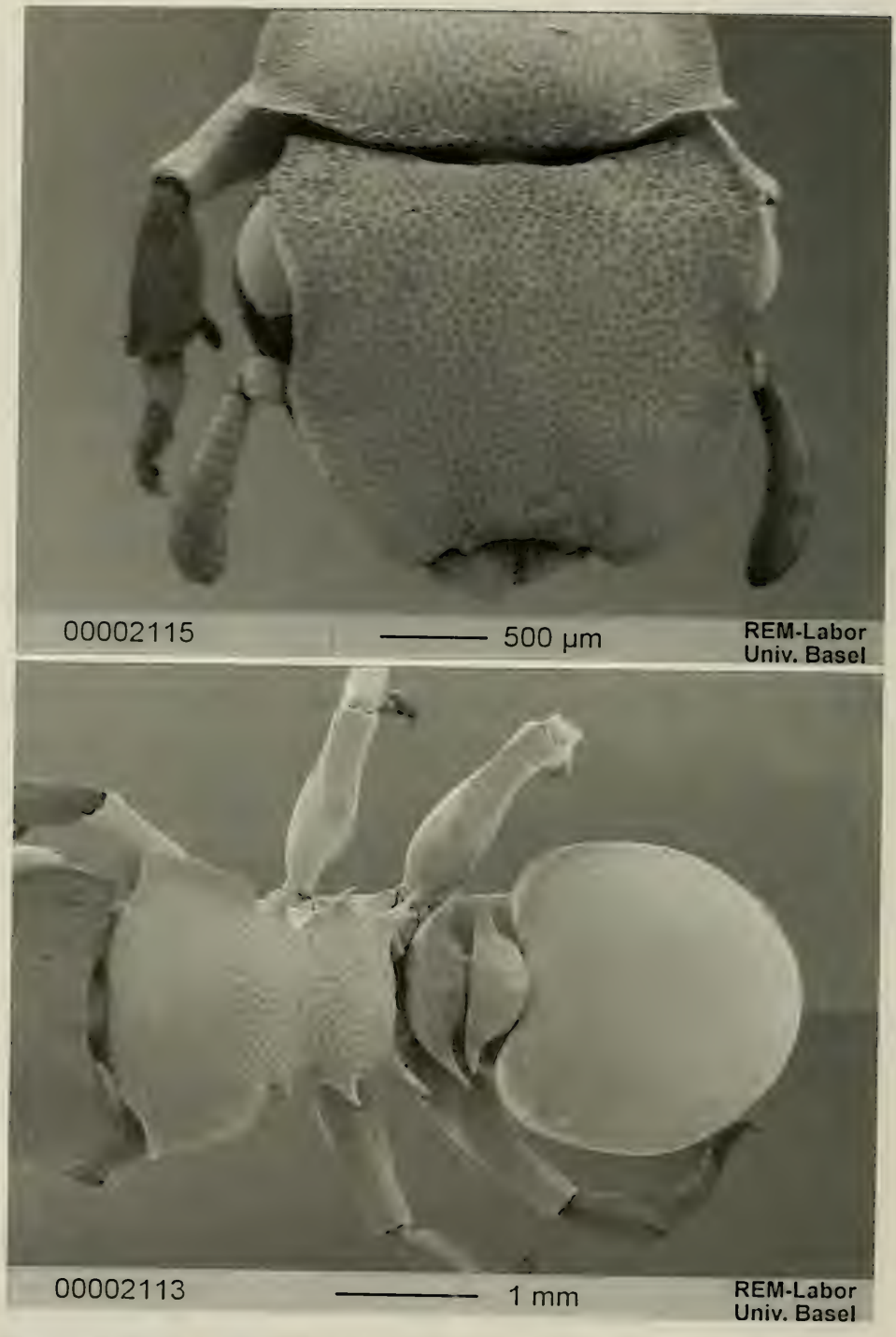


Fig. 108. *Cephalotes cordiventris* (SANTSCHI). Worker from Panama Canal Zone: head (top) and meso- and metasoma (bottom) in dorsal view.

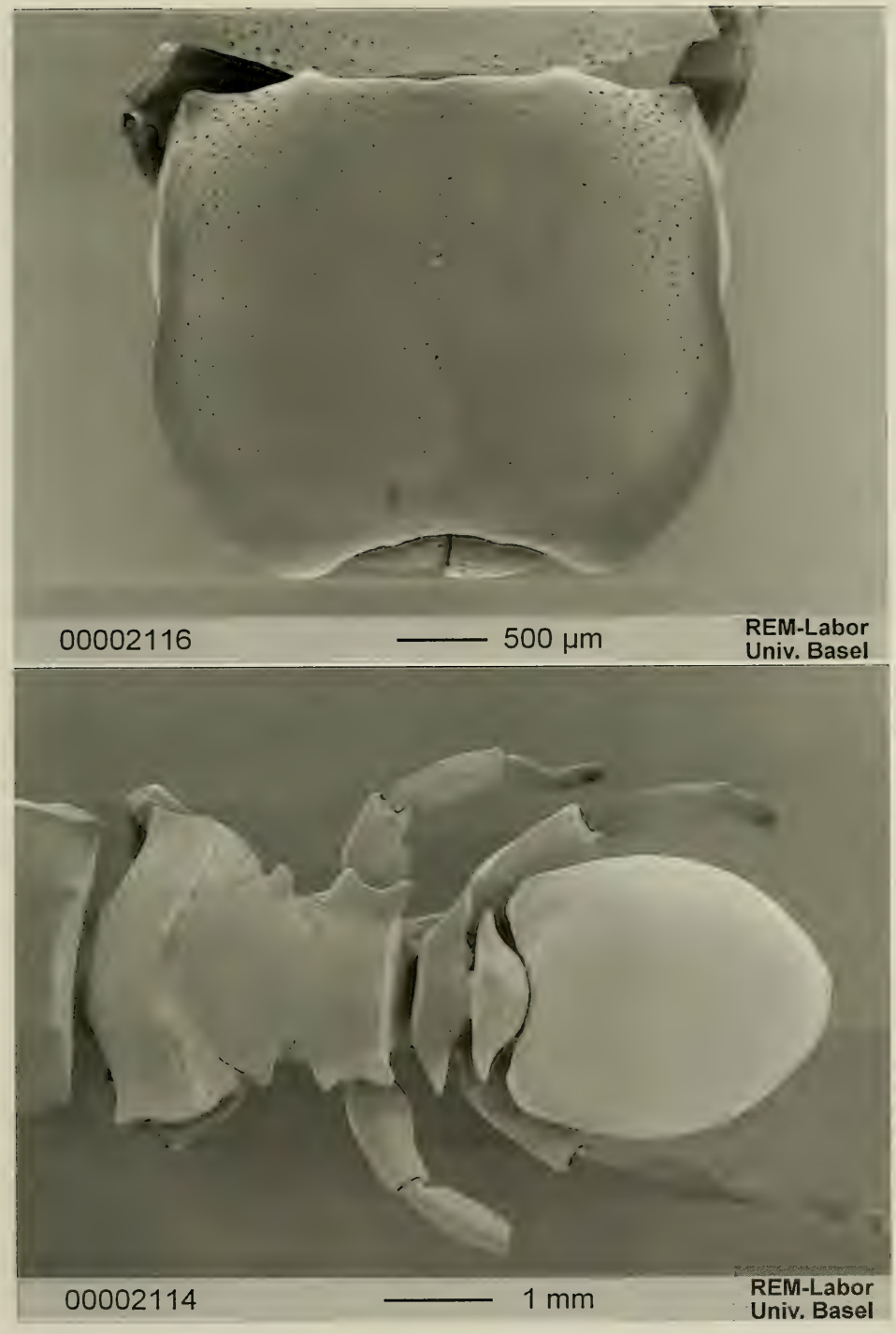


Fig. 109. *Cephalotes cordiventris* (SANTSCHI). Soldier from Panama Canal Zone: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 110. *Cephalotes cordiventris* (SANTSCHI). Gyne from Barro Colorado, Panama: head (top) and meso- and metasoma (bottom) in dorsal view.

Pilosity. Each fovea bearing an appressed hair of size proportional to the size of the fovea. Legs and posterior border of the gastral segments with erect, slightly clavate hairs. First gastral tergite anterolaterally covered by a spot of appressed hairs.

Colour. Shining black. First gastral tergite anterolaterally with a whitish-golden macula made out of a tuft of dense hairs.

Measurements (in mm) and indices: TL 8.44–10.20; HL 2.24–2.68; HW 2.56–3.08; EL 0.61–0.65; PW 2.56–3.04; PeW 1.52–2.00; PpW 1.32–1.68; HBaL 0.80–0.96; HBaW 0.30–0.36; CI 112.0–114.9; PI 100.0–101.3; PPeI 152.0–168.4; PPpI 180.9–193.9; HBaI 36.9–37.5.

G y n e (Fig. 110) (previously undescribed). - Head as in the soldier, but with the frontal carinae less broad and the eyes more convex. Ocelli far from the vertexal margin.

Mesosoma moderately convex in profile. Pronotal sides with short, obtuse humeral angles. Pronotal carina absent or superficially impressed on the sides. Mesonotum flat in side view. Lower mesopleurae with a lateral tooth. Sides of the basal face of the propodeum with two pairs of teeth separate by a superficial concavity, the first pair broad and triangular, the second longer than the first and with obtuse or pointed tips. Declivous face of the propodeum with posteriorly converging sides.

Petiole with distinctly differentiate anterior and posterior faces; anterior face truncate; posterior face sloping backwards. Petiolar sides with a broad, short, pointed, lateral spine directed backwards. Postpetiole convex, bearing in the middle of the node a superficial, incomplete "U" shaped carina; postpetiolar spines short, broad, arising from the anterior border of the postpetiole and directed laterally.

Gaster weakly protruding anterolaterally and with a marginate carina not reaching the stigma backwards.

Legs. As in the soldier but with narrower femora.

Sculpture. Head, pronotum and mesonotum minutely punctate and covered by small, superficial foveae smaller than their interspaces. Ventral part of the head, propleurae and basal face of the propodeum minutely and superficially punctate and with large, deep and dense foveae. Posterior face of the petiole, of the postpetiole, lower mesopleurae, distal half of the outer face of the femora and outer face of the tibiae minutely reticulate-punctate and with dense, oval foveae; this same type of sculpture but the foveae more round on the upper mesopleurae. Lateral and posterior border of the gastral tergites and posterior border of the sternites minutely reticulate. Remaining parts of the gaster shining and with small, superficial foveae denser on the anterolateral part of the first tergite. Legs superficially reticulate.

Pilosity. Each fovea bearing an appressed hair of size proportional to the size of the fovea. Legs and posterior border of the gastral segments with erect, slightly clavate hairs.

Colour. Shining black. First gastral tergite with a pair of yellowish-white, oval spots on the middle of the sides.

Measurements (in mm) and indices: TL 11.04–12.04; HL 2.32–2.60; HW 2.60–2.92; EL 0.60–0.64; PW 2.48–2.84; PeW 1.16–1.44; PpW 1.32–1.50; HBaL 1.04–1.08; HBaW 0.35–0.40; CI 112.1–112.3; PI 102.8–104.8; PPeI 197.2–213.8; PPpI 187.9–189.3; HBaI 33.6–37.0.

M a t e r i a l e x a m i n e d . - **Central America:** no further locality, 1 worker, STAUDINGER [MCZC].

Costa Rica: no further locality, 1 soldier, STAUDINGER [MCZC]; La Grenadilla, 1 worker, C. W. DODGE [MCZC]; 5 km N of Las Cañas, Guanacaste Prov., 45 m, on *Ctenosaura similis* carrion, 12.II.1968, 1 worker, BARNEY & CORNABY [USNM]; Tempisque, 22.I.1937, 1 worker, A. ALFARO [MZSP].

Panama: Bugaba, 1 worker, 1 soldier, 1 gyne, CHAMPION [MHNG, NHMB]; same locality, 800–1500 ft, 2 workers and 2 soldiers, CHAMPION [MCZC, MHNG]; Barro Colorado, 1 gyne, P. RAU [MCZC]; Canal Zone, 1930, 8 workers, 10 soldiers, (type series), BIERIG [NHMB]; San Francisco, 8.VI.1930, 8 workers, BIERIG [NHMB]; Juan Díaz, 02.VI.1930, 1 worker, 2 soldiers, BIERIG [NHMB].

D i s c u s s i o n . - This ant, originally described as a variety of *multispinus* (= *basalis*) and previously synonymised with it by KEMPF (1951), is emended as a good species in a personal communication of R. R. Snelling with which we entirely agree.

Cordiventris may be easily differentiated from *basalis* as follows: worker with narrower pronotal lamellae and first propodeal teeth angulate instead of pointed, soldier and gyne with reduced vertexal spines (instead of pointed denticles as in *basalis*). The limited material of gynes available (two for *cordiventris* and four of *basalis*) suggest important differences also in the size, position and colour of the gastral spots for which we refer to the relative descriptions. The sister species of *cordiventris* is *mompox* (see the diagnosis). According to the material we have been able to examine, *cordiventris* appears to occur only in Panama and Costa Rica, i. e. in complete but narrow allopatry with its sister species *mompox*, known only from Colombia and Venezuela. Given the great similarity between these two taxa, it may be interesting to check the morphology and microdistribution of specimens collected in or close to the contact zone.

None of the gynes we attribute to this species is certainly associated with workers or soldiers. The conspecificity between the gynes and neuters described here is nonetheless very probable for geographic reasons and is confirmed also by morphological similarities between the different specimens.

The report by CORNABY (1974) of unidentified Cephalotini feeding on carrion in Costa Rica refers to this species.

Distribution: Costa Rica, Panama.

Cephalotes mompox DE ANDRADE new species
Figs. 111, 388 (top)

Cryptocerus silvae FOREL, 1906: 234. Partim. Sta. Marta, Colombia mixed with workers of "*silvae*". Misidentification.

Cryptocerus multispinus (EMERY), FOREL, 1906: 234. Ouriheka, Colombia. Nec EMERY, 1894. Misidentification.

Derivatio nominis: "Mompox" is the name of one of the Indian tribes of north Colombia.

Type material: Holotype worker labelled: " Sta. Martha, Colombie (Forel)", in MHNG.

Diagnosis. - A member of the *basalis* clade characterised by the strong, longitudinal striae on the posterior face of the femora of the worker.

Worker (Figs. 111, 388 top). - Vertexal angles triangular. Vertexal margin concave, only laterally marginate and prolonged backwards as a "neck". Cheeks marginate inferiorly. Frontal carinae upturned over and slightly converging after the eyes. Eyes very large. Anterior clypeal border concave. Mandibles with lateral carinae.

Mesosoma convex in side view. Pronotum in dorsal view with the anterior border convex. Pronotum with a pair of broad lamellae, anteriorly pointed, medially straight and gently converging, and posteriorly round. Mesonotal teeth large and pointed. Pronotal and propodeal sutures in dorsal view impressed laterally only. Propodeum with differentiate basal and declivous faces; basal face with three pairs of teeth, the anterior pair small and obtuse, the median and the posterior pairs long and pointed; declivous face separate from the basal one by a superficial carina; sides of the declivous face converging posteriorly,.

Petiole anteriorly truncate. Petiolar sides almost completely occupied by the base of the petiolar spines which are long, pointed and curved backwards. Petiolar dorsum with a superficial transversal carina delimiting the anterior and posterior faces and with another longitudinal carina on the middle. Dorsum of the postpetiole gently convex and with a reduced longitudinal carina on the posterior half only. Postpetiolar spines pointed and arising from the anterior side of the postpetiole.

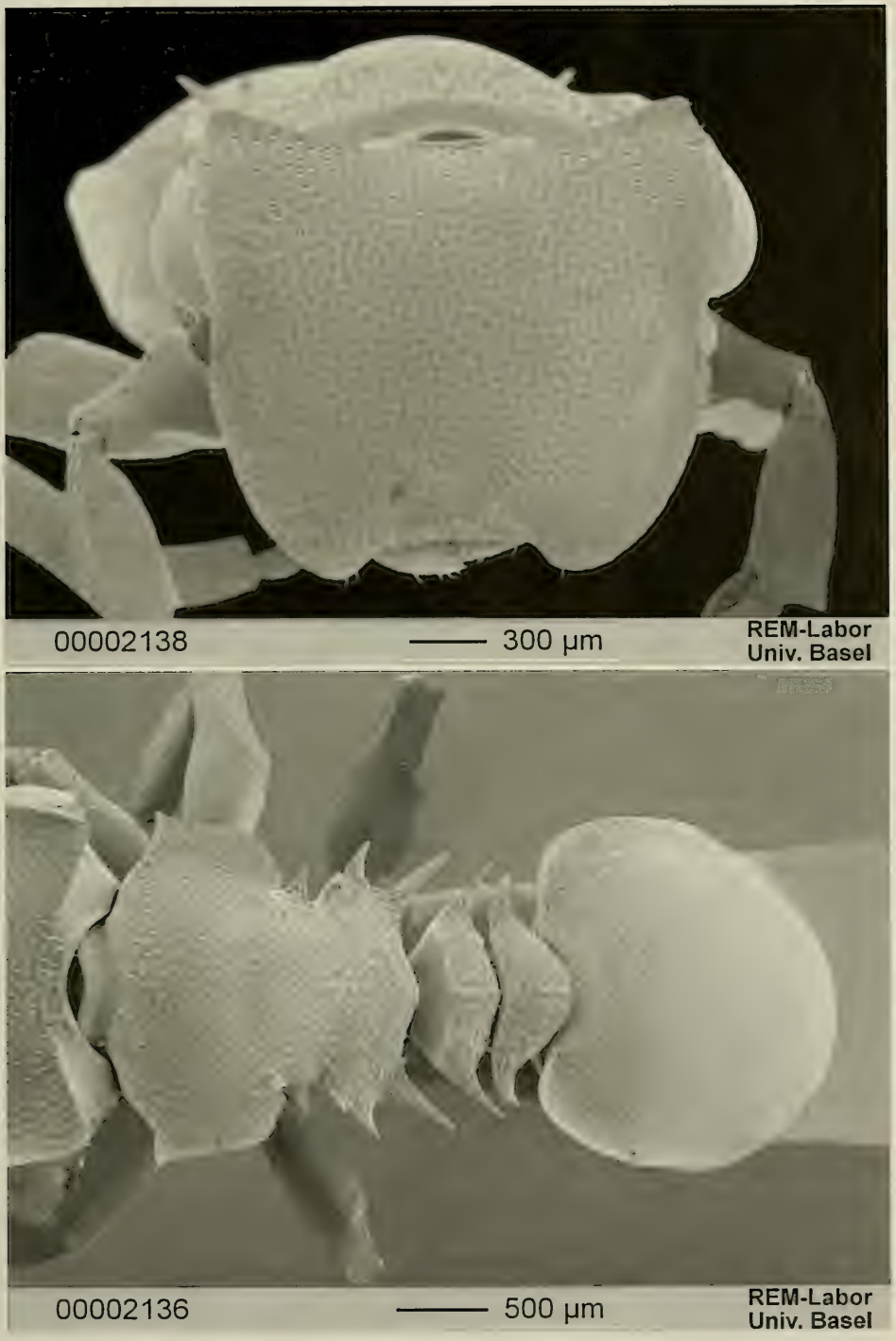


Fig. 111. *Cephalotes mompox* DE ANDRADE. Worker from Colombia (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Gaster round, with a broad, anterolateral lamella surpassing the gastral stigma posteriorly and continuing backwards as a thin carina up to the second third of the tergite.

Fore femora broader than the mid and hind ones. Fore femora dorsally with a marked longitudinal carina. Mid and hind femora with two medial teeth; mid and hind basitarsi laterally compressed and with broad base.

Sculpture. Head dorsum, mesosoma and pedicel minutely reticulate and covered with small foveae, oval and dense on the posterior fourth of the head, on the mesonotum and on the pedicel, sparser on the remaining parts of the head dorsum. Ventral face of the head minutely and superficially reticulate and with superficial, irregular foveae and irregular, thin, longitudinal rugosities, this sculpture less impressed on the ventral part corresponding to the vertexal angles. Dorsal third of the pleurae superficially reticulate and shining. Remaining part of the propleurae, declivous face of the propodeum and anterior half of the mesopleurae minutely reticulate, moderately shining, with rare, superficial foveae and with faint, thin, longitudinal rugosities. Remaining parts of the mesopleurae and metapleurae, distal half of the outer face of femora, outer face of the tibiae and first gastral tergite reticulate and with dense, oval foveae, more superficial on the gastral tergites. Anterior face of the femora, of the tibiae and tarsi superficially reticulate. Posterior face of the femora reticulate, with sparse, superficial foveae and covered with thick, longitudinal rugosities; the same type of sculpture but less impressed on the posterior face of the tibiae. First gastral sternite with superficial reticulation and shining medially. Few, thin, longitudinal rugosities on the sides of the first gastral sternite.

Pilosity. Each fovea with an appressed, thick, canaliculate hair. Border of the frontal carinae, of the pronotum, and legs with erect, short, rare, clavate hairs; similar hairs but slender and longer on the posterior border of the gastral tergites. Gastral sternites with minute, appressed, thin, pointed hairs and with rare, long, erect, thin pointed, hairs.

Colour. Black with the border of the pronotal lamellae and of the gastral lamellae ferruginous. Hairs whitish-golden.

Measurements (in mm) and indices: TL 6.52–7.56; HL 156–1.76; HW 1.98–2.28; EL 0.52–0.60; PW 1.88–2.16; PeW 1.20–1.52; PpW 1.08–1.28; HBaL 0.76–0.86; HBaW 0.29–0.33; CI 125.6–130.8; PI 100.0–108.5; PPeI 134.2–156.7; PPpI 151.6–180.0; HBaI 37.2–38.8

Material examined. - No locality, 1 worker [ZSMC].

Colombia: Caño del Tigre, Sept. 1943, 1 worker, ANDUZE [MCZC]; Ouriheca, 1896, 1 worker, FOREL [NHMB]; Hayes, 1 worker [NHMB]. Magdalena: San Pablo, 30.VII, 1 worker [ZSMC]; Santa Marta, 1 worker (holotype), FOREL [MHNG].

Venezuela: Zulia: Maracaibo, Botanical Garden, 23.IV.1981, 1 worker, A. S. MENKE & L. HOLLENBERG [USNM]. Apure: Haut Apure, Bois du Sarare, 1924, 1 worker, M. GRISOL [MNHN].

Discussion. - *C. mompox* is similar to *cordiventris*, but the worker of *mompox* can be easily separated from that of *cordiventris* by the presence of striae on the posterior face of the femora, the main apomorphy of *mompox*.

Since the three species *basalis*, *cordiventris* and *mompox* have been confused in the past, it is very likely that the Colombian specimens of "*multispinus*", a species of which we did not see Colombian specimens, and mentioned by KEMPF (1951) also are *mompox*. FERNÁNDEZ et al. (1996) also report "*C. multispinus*" from the Colombian states of Chocó, Huila and Norte de Santander.

Distribution: Colombia, Venezuela.

Cephalotes femoralis (SMITH) new combination

Fig. 112

Cryptocerus femoralis SMITH, 1854: 219. Worker. Original description. Type locality: Colombia. Type material probably lost; neither in BMNH nor in OXUM.

Cryptocerus silvae FOREL, 1906: 233. Partim. Worker. Synonymy by KEMPF, 1951: 202. Type localities Santa Marta, Sabanilla, Cienaga, Calabasio, Ouriheka (Colombia). Type mate-

rial: 13 syntype workers labelled "*Cr. silvae*, Sta. Martha, Colombie, Forel", in MHNG, examined; one syntype worker same data as before in NHMB, examined; 4 syntype workers labelled "*Cr. silvae*, Sabanilla, Santschi", in MHNG, examined. Lectotype selected by KEMPF (1951) not found in MHNG. See also *mompox*.

Paracryptocerus femoralis (SMITH), KEMPF, 1951: 202, fig. 129. Worker. First combination in *Paracryptocerus*.

Zacryptocerus femoralis (SMITH), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *basalis* clade the worker of which is characterised by the first gastral tergite covered with thin, irregular, longitudinal rugosities and by the frontal carinae, orange.

Worker (Fig. 112) (description of KEMPF, 1951). - "Length 6.6 mm. Median head length 1.56 mm; Weber's length of thorax 2.07 mm. Black; the following ferruginous: tip of mandibles, frontal carinae, lateral border of pronotal plates. Tip of last funicular segment orange.

Head subopaque, subtrapezoid. Mandibles finely reticulate-punctate, finely reticulate-rugose. Sides of head greatly sinuate, distinctly converging in front, conspicuously expanded above the eyes. Frontal carinae prolonged behind the scrobe, upturned above the eyes, reaching the angulate occipital corner. Occipital border concave, sharply crested laterad, the middle piece slightly convex. Upper surface of head very little convex, finely reticulate-punctate, densely foveolate discally, reticulate-rugose and foveolate laterad and caudad, each foveola containing a broad, appressed, short, canaliculate, silvery scale. Cheeks strongly marginate beneath, densely covered with large silvery appressed scales. Lower surface of head reticulate-rugose and foveolate, rather densely scaled.

Thorax subopaque. Sides of lateral pronotal plates subparallel, the anterior angle subrectangular, the posterior corner rounded. Promesonotal suture obsolete. Mesonotum with a strong lateral spine. Mesoepinotal suture obsolete.

Basal face of epinotum with a broad, plate-like triangular tooth, having on its anterior border a smaller accessory denticule, on each side, and a posterior, short, acuminate spine, projecting obliquely backward and upward, shorter than the length of the basal face. Promesonotum somewhat convex in profile. Declivous face coarsely longitudinally striated, its sides subemarginate. Dorsum of thorax finely reticulate-punctate, coarsely reticulate-rugose, densely scaled below, smooth above. Femora, even the fore femora, greatly incrassated and compressed, angulate above the lateral faces rather densely reticulate-punctate longitudinally rugulose and subopaque. Tibiae prismatic. Hind basitarsus broader and shorter than in *multispinus* [= *basalis*].

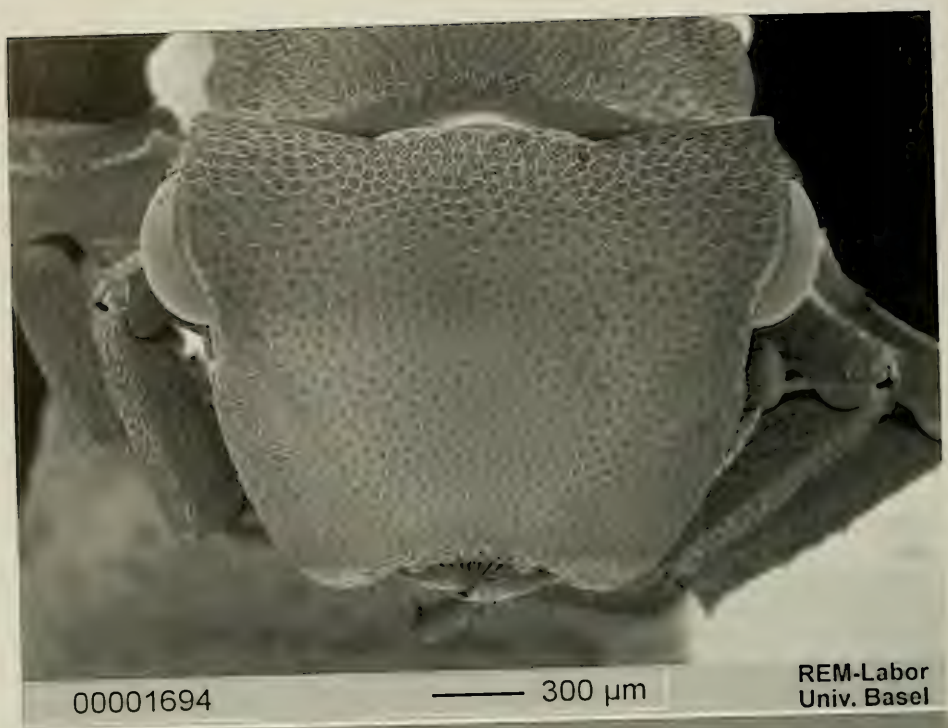
Petiole and postpetiole subopaque. The petiolar spines less upturned than in *multispinus* [= *basalis*]. Both segments above with a median longitudinal carinule, which in the postpetiole arises from a median tooth on the anterior border.

Gaster subopaque; broadly subcordiform; very convex above. First gastral tergite scarcely emarginate in front mesad, narrowly crested antero-laterad, rather conspicuously longitudinally areolate-rugulose, not foveolate, without distinctly visible scales. Longitudinal rugulae very distinct on base and apical third of the tergite. First sternite with coarse longitudinal striae laterad. Sparse, erect hair on the apical third of the gaster."

Measurements (in mm) and indices: TL 6.08–6.92; HL 1.48–1.68; HW 1.92–2.24; EL 0.5–0.56; PW 1.68–2.00; PeW 1.28–1.56; PpW 1.16–1.40; HBaL 0.60–0.72; HBaW 0.28–0.34; CI 129.7–136.8; PI 110.9–120.1; PPeI 124.3–134.4; PPpI 142.8–148.4; HBaI 46.7–50.0.

Material examined. - **Colombia**: Sabanilla, 4 workers (syntypes), SANTSCHI [MHNG]. Magdalena: no further locality, 1 worker [ZSMC]; no further locality, 1 worker, FEILHMAN (?) [NHMB]; Río Frío, March 1924, 1 worker, W. M. MANN [MZSP]; Santa Marta, 14 workers (syntypes), FOREL [MHNG, NHMB]. Atlántico: Puerto Colombia, 1932, 2 workers [USNM].

Venezuela: Zulia: Carrasquero, 29–30.V.1976, 1 worker, A. S. MENKE & D. VINCENT [USNM].



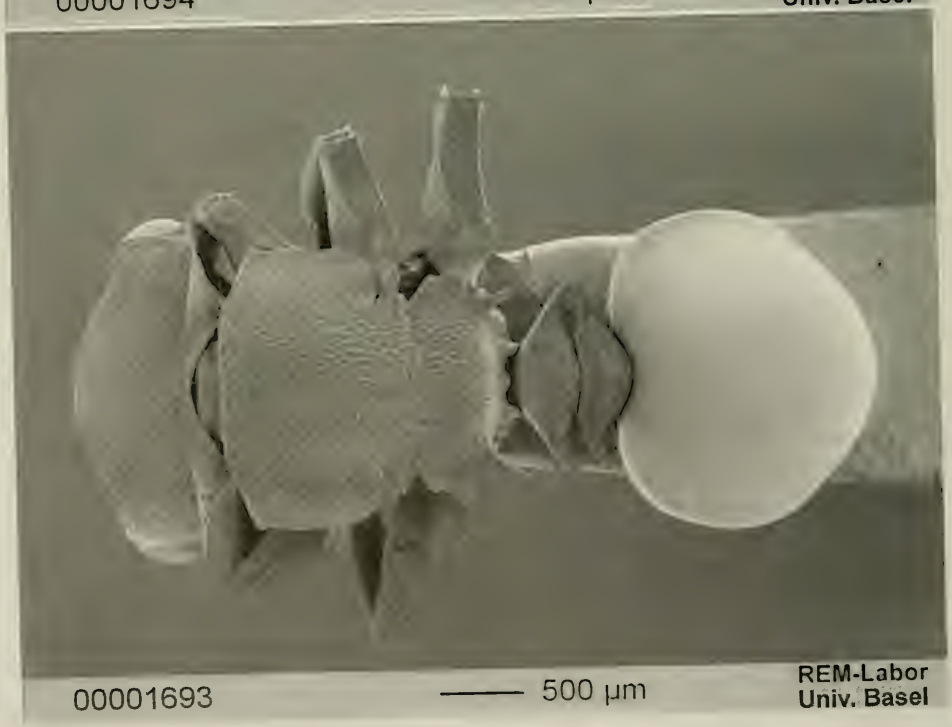


Fig. 112. *Cephalotes femoralis* (SMITH). Worker from Carrasquero (Zulia), Venezuela: head (top) and meso- and metasoma (bottom) in dorsal view.

D i s c u s s i o n . - *C. femoralis* is the species with the most visible apomorphies within the *basalis* clade. It can be easily recognised from all the other species by the thin, longitudinal, irregular rugosities on the first gastral tergite. The worker of *C. femoralis* shares with those of *basalis* and *inca* the long petiolar spines and the two pairs of anterior propodeal teeth flat and broad.

Large workers of *femoralis* have the posterior face of the femora with superficial, irregular, longitudinal rugosities; the same structure is also present in *mompox* but the rugosities in this species are much more impressed and are present in workers of all sizes.

FERNÁNDEZ et al. (1996) report this species from the Colombian state of Bolívar.

D i s t r i b u t i o n : Colombia, Venezuela.

Cephalotes basalis (SMITH) new combination

Figs. 113, 114, 115, 116, 117, 118

Cryptocerus basalis SMITH, 1876: 608. Gyne. Original description. Type locality: Chontales (Nicaragua), erroneously given as Brazil. Type material: holotype gyne in BMNH, labelled as type, „Braz.", with the reference number 70 59, examined.

Cryptocerus cordatus multispinus EMERY, 1890: 75, pl. 9 fig. 5. Worker. Original description. Type locality: Costa Rica. Type material: one syntype worker in the Museo Regionale di Scienze Naturali, Torino (CASOLARI & CASOLARI MORENO, 1980: 84), not available for the present study; 5 workers from Jiménez, Alajuela and S. José (Costa Rica) in MCSN, examined. 6 syntype workers and one syntype soldier (Costa Rica) in MCSN and MHNG, examined. Synonymy suggested by R. R. SNELLING, personal communication, confirmed by our examination of the type material. N e w s y n o n y m .

Cryptocerus multispinus EMERY, EMERY, 1894 a: 203, pl. 3 fig. 1. Soldier.

Cryptocerus multispinus EMERY, FOREL, 1899 a: 49, pl. 3 fig. 11. Gyne, nec worker and soldier.

Paracryptocerus multispinus (EMERY), KEMPF, 1951: 204, figs. 133, 137. Worker and soldier. First combination in *Paracryptocerus*.

Paracryptocerus multispinus (EMERY), WHEELER & WHEELER, 1954 b: 155, figs. 45, 46. Larva.

Zacryptocerus multispinus, JEANNE, 1979: 1224. First combination in *Zacryptocerus*.

Zacryptocerus basalis, HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

Zacryptocerus cristatus, HESPENHEIDE, 1986: Fig. 1. Worker. Misidentification.

D i a g n o s i s . - A member of the *basalis* clade characterised, in the worker, by the pronotal lamellae anteriorly and posteriorly obtuse and by the petiolar spines shorter than the basal face of the propodeum, and, in the soldier and gyne, by the vertex with a pair of developed spines.

W o r k e r (Fig. 113) (description of KEMPF, 1951 sub *multispinus*). - „Length 7.1 mm. Median head length 1.75 mm; Weber's length of thorax 2.34 mm. Black.

Head subopaque, subquadrate. Mandibles finely reticulate-punctate, finely reticulate-rugose. Sides of head sinuate, conspicuously converging in front, concave in front of, convex and visibly upturned above, the eyes. Frontal carinae prolonged behind the scrobe, as a visible carina, which reaches the sharply angulate, subspinose occipital corner. Occipital border concave, sharply crested laterad, the middle piece slightly convex. Upper surface of head little convex, finely reticulate-punctate, densely foveolate, each foveola containing a broad, appressed, short, canaliculate, silvery scale. Cheeks strongly marginate beneath, densely covered with large silvery scales. Lower surface of head more fulgid, sparsely scaled.

Thorax subopaque. Sides of lateral pronotal plates converging behind, the anterior angle acute, subspinose, the posterior angle subrectangular. Promesonotal suture obsolete. Mesonotum with a strong, lateral spine. Mesoepinotal suture vestigial. Basal face of epinotum with a broad, plate-like, triangular, lateral tooth, with an accessory smaller tooth arising from its

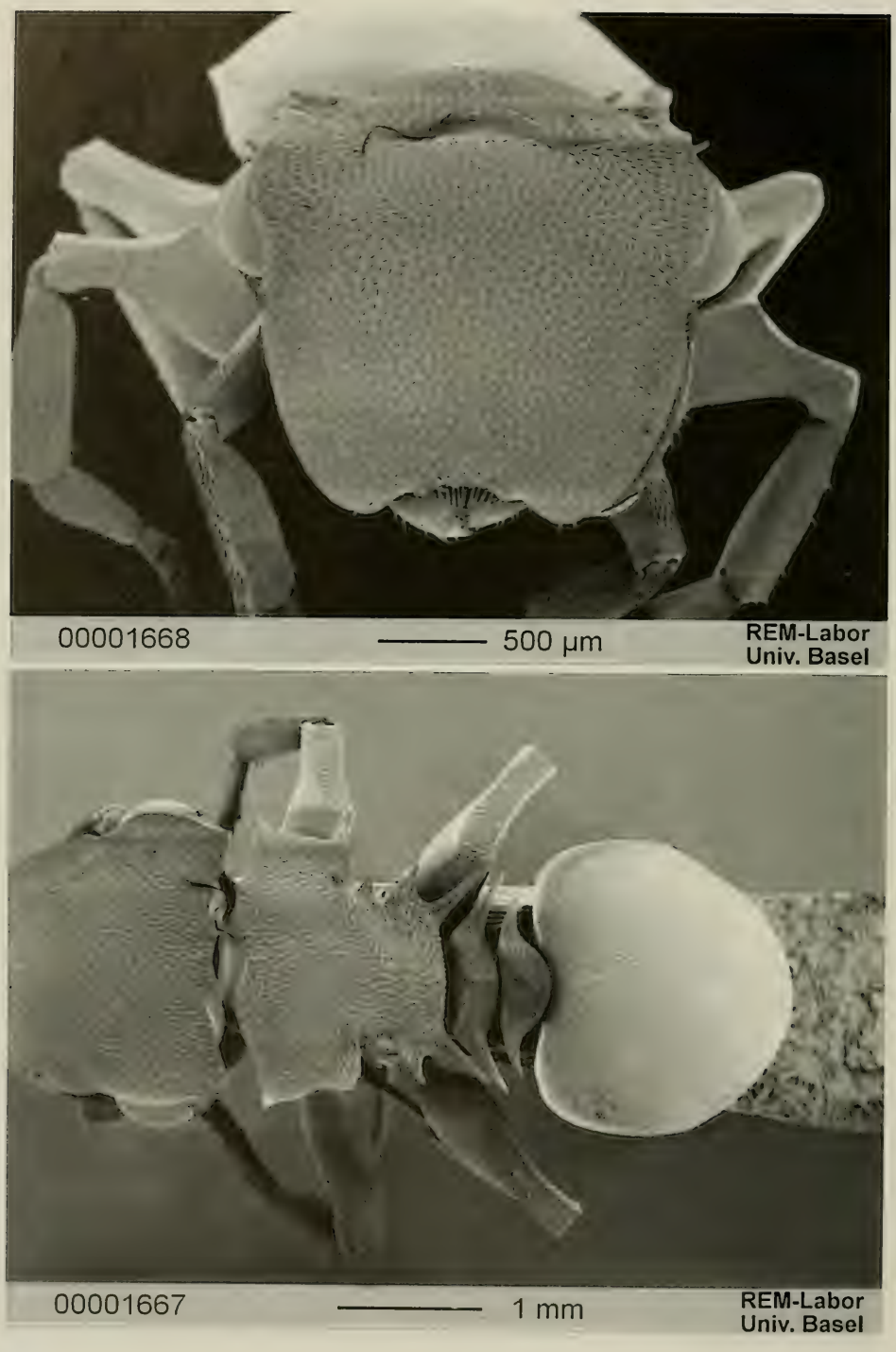


Fig. 113. *Cephalotes basalis* (SMITH). Worker from Bristol, Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

anterior border, and a longer, subacuminate, posterior spine, projecting obliquely backward and slightly upward, subequal to the length of the basal face. Promesonotum somewhat convex in profile. Dorsum of thorax finely reticulate-punctate and foveolate, each foveola containing an appressed canaliculate scale, as on head. Laterotergite of pronotum longitudinally striated. Sides of thorax densely scaled below, smooth above. Declivous face of epinotum finely reticulate, very finely and distantly longitudinally rugulose, its sides marginate. Femora slightly less inflated than in *femoralis*, the posterior side only finely reticulate, and subfulgid. Hind basitarsus elongate, broadened and flattened proximad.

Petiole and postpetiole subopaque, sculptured as upper surface of thorax, with a median longitudinal carinule above, arising on the postpetiole distinctly behind the anterior border which is slightly impressed mesad. Petiole with very long, slightly raised, lateral spines.

Gaster subopaque, broadly cordiform, very convex above. First gastral tergite slightly emarginate in front mesad, crested antero-laterad, sculptured as dorsal surface of thorax, foveolae more or less obsolete, but similarly scaled; scales large, canaliculate. First sternite with a few longitudinal rugosities on the sides. Erect hair confined to the terminal tergites and the sternites of the gaster, and few erect setulae on the internal curvature of the frontal carinae."

Measurements (in mm) and indices: TL 5.96–7.20; HL 1.42–1.72; HW 1.72–2.20; EL 0.48–0.56; PW 1.68–2.12; PeW 1.28–1.68; PpW 1.08–1.40; HBaL 0.63–0.85; HBaW 0.22–0.29; CI 121.1–130.6; PI 101.9–108.5; PPeI 126.2–139.4; PPpI 150.0–170.4; HBaI 31.8–42.0

S o l d i e r (Fig. 114) (description of KEMPF, 1951 sub *multispinus*). - "Length 10 mm. Median head length 2.73 mm; Weber's length of thorax 2.93 mm. Black.

Head subfulgid, subquadrate. Mandibles finely reticulate, almost smooth, sparsely foveolate. Frontal carinae rounded anteriorly, slightly raised laterally, continued behind the scrobe as a distinct carina, reaching the occipital corner. Upper surface of head little convex, vertex with two short teeth above the truncate occiput, which is submarginate above mesad and laterad. Cheeks marginate beneath, with a strong carina extending back to the occipital corner, densely foveolate and scaled. Upper and lower surface of head smooth, covered with small foveolae. Lower surface of head superficially reticulate, the foveolae sparser containing a distinctly visible hair.

Thorax fulgid. Pronotum greatly expanded laterad, the anterior border scarcely arcuate, the lateral borders subparallel, sharply crested, converging mesad, behind the conspicuous, medially interrupted, transverse pronotal crest. Promesonotal suture distinct. Mesonotum with a strong lateral apically rounded tooth. Mesoepinotal suture impressed, greatly arcuate caudad. Basal face of epinotum with a strong, broad triangular tooth on each side, and a posterior strongly divergent, somewhat upturned apically, stout spine the posterior border of which is continuous with the marginate posterior border of the basal face. Dorsum of thorax and laterotergite of pronotum mostly smooth, vestigially and very finely reticulate, sparsely foveolate, the foveolae larger, rather dense, containing visible scales on epinotum. Sides of thorax mostly smooth, with a patch of very dense silvery scales on mesopleura and metapleura. Declivous face perpendicular to basal face, smooth and fulgid.

Petiole with smooth anterior truncate face, which is marginate above. Lateral spines greatly upturned, upper face densely scaled and foveolate. Postpetiole narrower than petiole, lateral spines not upturned. Sculpture as on petiole.

Gaster fulgid above, subfulgid below. Broadly cordiform, slightly emarginate in front mesad, narrowly crested antero-laterad. First gastral tergite with dense large canaliculate scales on the anterior corners and on the apical third, scales and foveolae more or less obsolete discad. Sternites finely reticulate, more sparsely scaled. Erect hair confined to apical third of gaster."

Measurements (in mm) and indices: TL 8.48–9.52; HL 2.12–2.642; HW 2.76–3.16; EL 0.60–0.65; PW 2.60–3.00; PeW 1.68–2.00; PpW 1.46–1.60; HBaL 0.79–0.84; HBaW 0.32–0.35; CI 119.7–130.2; PI 104.0–108.8; PPeI 142.8–164.4; PPpI 178.1–189.7; HBaI 40.0–43.7.

G y n e (Fig. 115). - Head convex. Frontal carinae broadly expanded anteriorly, slightly converging before the eyes, slightly upturned over them, and ending in an obtuse tooth on the vertexal angles. Vertex with a pair of thick teeth connected by a faint carina. Mandibles laterally carinate.

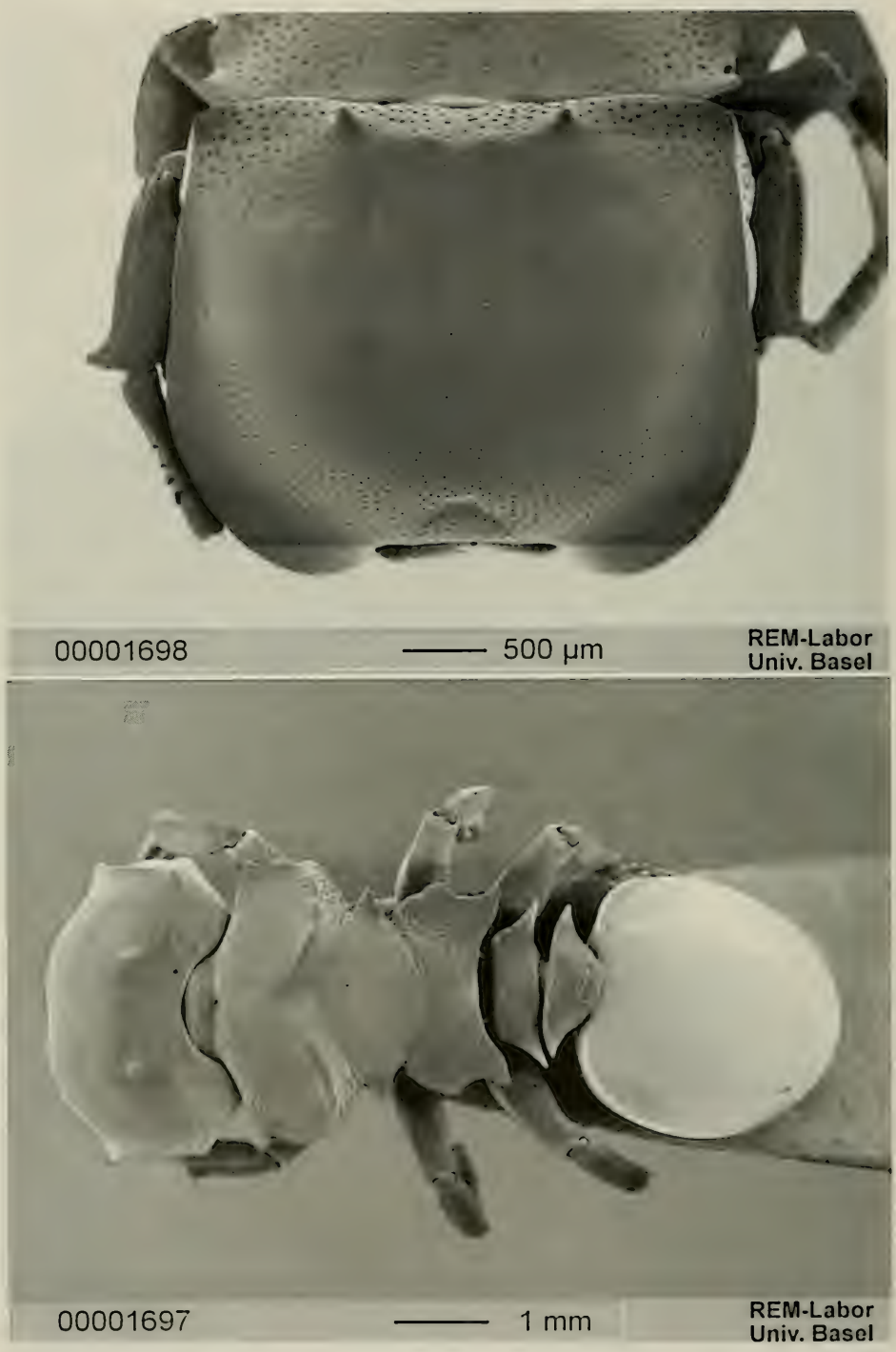


Fig. 114. *Cephalotes basalis* (Smith). Soldier from Puerto Viejo (Heredia), Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

Mesosoma almost flat in profile. Humeral angles with a short, obtuse tooth. Pronotal carina concave and marked on the sides, convex and faint in the middle. Mesonotum and scutellum flat in side view. Lower mesopleurae with a lateral tooth. Sides of the basal face of the propodeum with two pairs of teeth separate by a concavity, the first pair short, triangular, the second one long and pointed. Declivous face of the propodeum with converging sides posteriorly.

Petiole with distinctly differentiated anterior and posterior faces; anterior face oblique with gently convex anterior border; posterior face sloping backwards, with a pair of pointed lateral spines, half of the petiolar length and directed backwards. Postpetiole broadly convex in the middle, and bearing a faint, incomplete "V" shaped carina; postpetiolar spines arising from the anterior border of the postpetiole and directed laterally.

Gaster marginate anteriorly by a strong carina not surpassing the stigma backwards.

Legs. Mid and hind femora angulate. Mid and hind basitarsi flat and broad at the base.

Wings as in Fig. 116.

Sculpture. Head dorsum minutely punctate and covered with small, superficial foveae smaller than their interspaces. Mesosoma and pedicel superficially punctate, superficially shining, with foveae larger than those on the head dorsum, sparser on the anterior half of the pronotum and mesonotum, denser on the posterior half of the pronotum, on the scutellum, on the propodeum, on the pedicel and on the mesopleurae. Ventral face of the head and propleurae with large foveae and almost shining. Metapleurae, declivous face of the propodeum, anterior face of the petiole, gaster and legs superficially reticulate-punctate and slightly shining. Small, sparse, superficial foveae on the centre of the anterior fourth of the first gastral tergite, on the first gastral sternite and on the legs, denser on the sides of the anterior fourth of the first gastral tergite and on the remaining gastral segments.

Pilosity. Each fovea bearing an appressed, canaliculate hair, of thickness proportional to the size of the foveae. Gaster, except the centre of the first tergite, distal part of femora, outer face of the tibiae with dense, appressed, thick canaliculate hairs. Apex of the gaster with long, erect, truncate hairs, rare on the legs.

Colour. Black. Anterior third of the first gastral tergite with an orange spot on each side.

Measurements (in mm) and indices: TL 11.72–13.07; HL 2.64–2.72; HW 2.72–2.96; EL 0.60–0.65; PW 2.76–3.00; PeW 1.64–1.76; PpW 1.56–1.80; HBaL 0.90–1.08; HBaW 0.35–0.38; CI 107.8–108.8; PI 95.9–104.2; PPeI 165.9–186.5; PPpI 162.2–182.9; HBaI 35.2–38.9.

M a l e (Fig. 117) (previously undescribed). - Head (eyes included) about 1/3 broader than long; vertexal margin superficially carinate, straight in the middle and curved laterally, diverging into two obtuse angles. Vertex and ocelli protuberant. Eyes broadly convex, in the middle of the sides of the head. Frontal carinae not raised and shortly diverging backwards. Frons gently convex and separate from the clypeus by a superficial furrow. Clypeus convex, its anterior face almost truncate. Mandibles with a superficial lateral carina. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with a slightly marked scapular angle and broadening backwards. Mesonotum convex; median Mayrian carina and parapsidal furrows weakly impressed.

Scutellum convex, its sides converging posteriorly. Propodeum with differentiate basal and declivous faces; basal face with the sides gently convex and converging posteriorly towards the declivous face, the latter converging posteriorly with the lateral carinae.

Petiole slightly narrower than the postpetiole, with truncate and medially concave anterior face and with the posterior face sloping backwards; petiolar sides with a small, obtuse denticle medially. Postpetiole convex dorsally; postpetiolar sides with a small, pointed denticle anteriorly and converging posteriorly.

Gaster narrower than the mesosoma.

Genitalia and subgenital plate as in Fig. 118.

Wings as in the gyne.

Fig. 115. *Cephalotes basalis* (SMITH). Gyne from Puerto Viejo (Heredia), Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 116. *Cephalotes basalis* (SMITH). Gyne from Puerto Viejo (Heredia), Costa Rica, fore and hind wings

Sculpture. Head, propleurae and pedicel reticulate and with small, superficial foveae dense on the vertexal angles, on the frons and on the sides of the pedicel, rare close to the eyes, on the propleurae and on the dorsum of the pedicel. Mesosoma reticulate and with deeper and larger foveae than on the frons. Propodeum with irregularly longitudinal rugosities. Mesopleurae anteriorly superficially reticulate and with dense, superficial, small foveae, this sculpture less impressed posteriorly. Metapleurae feebly shining, with longitudinal rugosities on the lower part. Gaster and legs reticulate, the reticulation less impressed on the legs and on the first gastral sternite.

Pilosity. Head, mesosoma and pedicel covered by dense, long, suberect hairs; similar hairs but sparse on the posterior border of the tergites, of the sternites and on the legs. Gaster and legs with appressed, thin, short hairs.

Colour. Head and mesosoma black, pedicel lighter. Gaster and femora ferrugineous. Remaining parts of the legs yellowish.

Measurements (in mm) and indices: TL 6.36–7.10; HL 0.96–1.04; HW 1.24–1.36; EL 0.56–0.57; PW 1.48–1.64; PeW 0.56–0.60; PpW 0.64–0.68; HBaL 0.72; HBaW 0.12; CI 130.8–135.5; PI 82.9–83.8; PPeI 264.3–273.3; PPpI 231.2–241.2; HBaI 16.7.

Material examined. - **Mexico**: no further locality, 1 worker [MNHN]. Colima: Vulkan, 10.VIII.1918, 1 worker, Joh. LAUE [ZSMC]. Chiapas: Palenque, rain forest and ruins, 18.VI.1982, 1 worker, F. COYLE [MCZC].

Guatemala: Escuintla, 27–28.XII.1911, 5 workers, 1 soldier, 1 gyne, W. M. WHEELER [MCZC]; Patulul, 1 worker [MHNG]; same locality, 07.I.1912, 1 worker, 1 soldier, W. M. WHEELER [MCZC]; Sololá, Pacific slope, 3900 ft, 05.IX.1908, 1 worker [MCZC].

Honduras: Tela, 25.IV.1923, 1 worker, S. C. BRUNER [USNM].

El Salvador: Los Aguilares, 23.VI.1958, 1 worker [USNM]; Prov. San Salvador, Lago de Ilopango, N side, 05.IV.1973, 1 worker, R. SILBERGLIED [USNM].

Fig. 117. *Cephalotes basalis* (SMITH). Male from Puerto Viejo (Heredia), Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

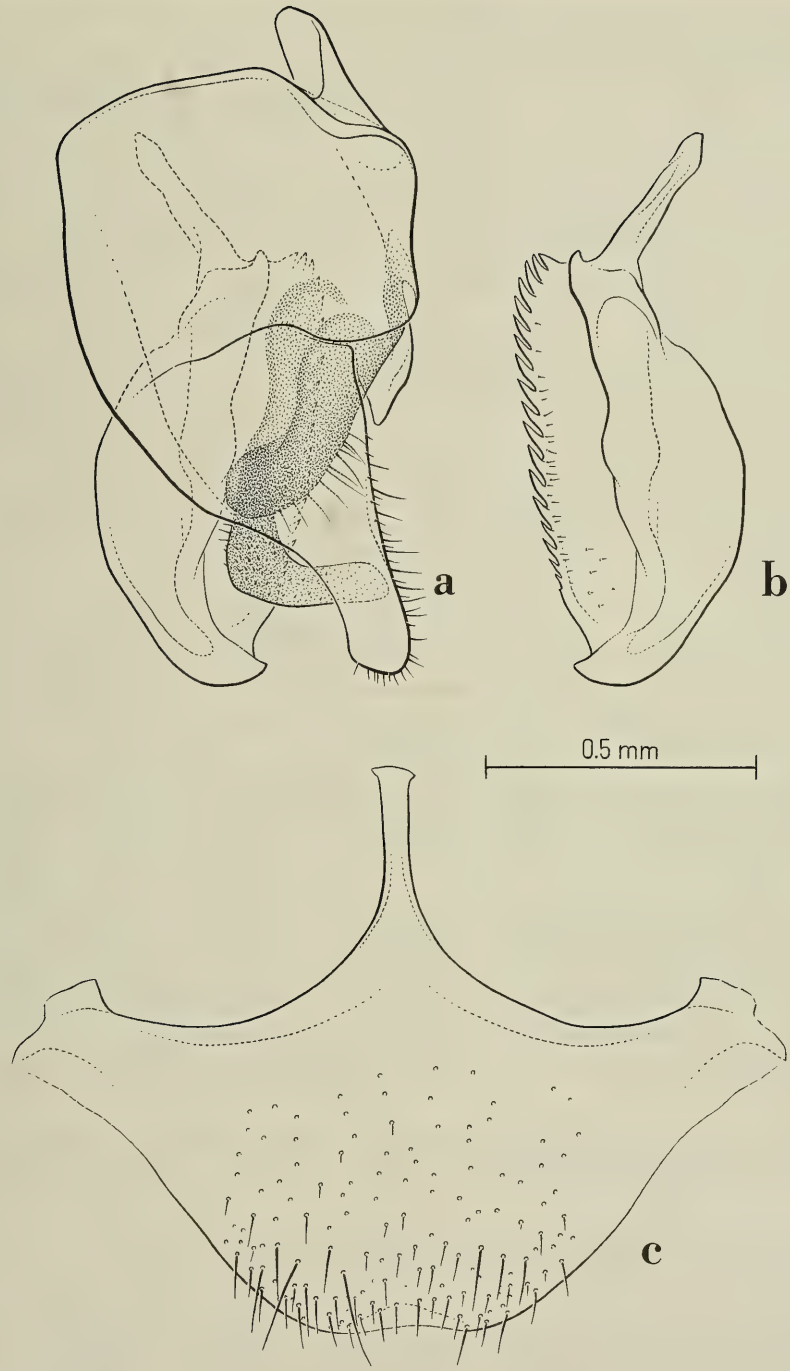


Fig. 118. *Cephalotes basalis* (Smith). Male from Puerto Viejo (Heredia), Costa Rica. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Nicaragua: no further locality, 2 workers [USNM]; Granada, 1 worker, BAKER [MCZC]; Managua, Low R. Finzi, 1950, 2 workers, RURCH [MCZC].

Costa Rica: no further locality, 6 workers, 1 soldier (all syntypes) [MCSN, MHNG]; no further locality, 2 workers, 4 soldiers, F. NEVERMANN [MCZC, MZSP]; Turrialba, 1 worker [MCZC]; Bristol, VIII.1956, 4 workers, LARA [MZSP]; Desmonte, 1 worker, A. BIERIG [MZSP]; L. Diamantes, 1 gyne [USNM]; Jiménez, 1 worker (syntype) [MCSN]; Alajuela, 2 workers (syntypes), ALFARO [MCSN]; same locality, Prov. Florencia, 11 mi N, 06.VII.1963, 1 worker, D. H. JANZEN [USNM]; San José, III.1895, 1 worker [MCSN]; Heredia, Prov. Puerto Viejo, 08.VIII, 11.VIII.1965, 4 workers, 2 soldiers, 2 gynes, 4 males, F. COYLE [MZSP]; Finca La Selva, 21.IV.1979, 2 workers, 1 soldier, L. GARLING [MCZC]; Pen. Osa, Par. Nat. Corcovado, Sirena, 8°28' N, 83°35' W, 31.V.1982, 0–100 m, 2 workers, J. LONGINO [MCZC].

Panama: Bugaba, 2 workers, CHAMPION [MHNG]; same locality, 800–1500 ft., 1 worker, CHAMPION, Ex. GODMAN & SALVIN [MCZC]; Barro Colorado Is., Canal Zone, Feb.-Mar. 1943, 1 worker, ZETEK 50–59 [USNM]; same locality, 20–21.VI.–24.VII.1924, 10 workers, 6 soldiers, N. BANKS [MZSP]; same locality, I. 1960, 1 worker, W. L. BROWN & E. S. MCCLUSKEY [MCZC]; same locality, 16 workers, 1 soldier, 25.VI.1924, W. M. WHEELER [MCZC, MZSP]; same locality, 10 workers, W. C. ALLEE [MCZC]; Bella Vista, 06.VII.1924, 1 worker, N. BANKS [MCZC]; Canal Zone, 4 mi NW Gamboa, 23.II.1975, 1 worker, LAWRENCE & ERVIN [MCZC]; Canal Zone, Gatun, 13.XI.1911, 2 workers, WHEELER [MCZC]; Río Perequete, Chorrera, 18–20.III.1991, 1 worker, D. QUINTERO [CPCC].

Ecuador: Pichincha: Sto. Domingo, VIII.IX.1930, 1 gyne, R. BENOIST [MNHN].

Discussion. - The workers from Guatemala collected by WHEELER differ from those of other localities by the denser foveae on the body, by the frontal carinae less upturned over the eyes and by the broader propodeum, and, the soldiers and the gyne from the same locality, by the much higher pronotal crest, by the larger spines on the vertex and by the broader propodeum.

All specimens (workers and soldiers) from Barro Colorado, Panama Canal Zone, collected by BANKS and WHEELER differ from other specimens from Barro Colorado and from other localities for the broader pronotal lamellae and for the petiolar spines curved downwards. A specimen of unknown provenance and with the same morphological configuration has been figured by HESPENHEIDE (1986) under the name of *Zacryptocerus cristatus*. A gyne from Ecuador has the petiolar spines similar to those of the workers and soldiers from Barro Colorado. KEMPF (1951, 1972) reports this species from Colombia, a country from which we saw no specimens. On the contrary, superficially similar Colombian material from three different localities we have been able to study is described in this paper as *C. mompox*.

Distribution: Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Colombia?, Ecuador.

Cephalotes inca (SANTSCHI) new combination

Figs. 119, 120, 121

Cryptocerus inca SANTSCHI, 1911: 278. Worker. Original description. Type locality: La Massa (sic) (Peru). Type material: three syntype workers labelled "Muséum Paris, Pérou, La Masa, (400 m. d'alt.), P. Rivet 1906", 2 in NHMB, 1 in MHNG, examined.

Paracryptocerus multispinus inca (SANTSCHI), KEMPF, 1951: 208, fig. 134. Worker. First combination in *Paracryptocerus*.

Paracryptocerus inca (SANTSCHI), KEMPF, 1967: 362.

Zacryptocerus inca (SANTSCHI), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *basalis* clade characterised, in the worker, by the frontal carinae upturned over the eyes, by the vertexal angles with triangular tooth, by the pointed anterior and posterior border of the pronotal lamellae, and by the length of the propodeal and petiolar spines, both longer than the basal face of the propodeum, and, in the gyne, by the secondary loss of the gastral coloured spots.

W o r k e r (Fig. 119). - Vertexal angles triangular. Vertexal margin concave, only laterally marginate and medially with a short "neck". Cheeks completely marginate inferiorly. Frontal carinae strongly upturned over and converging after the eyes. Eyes very large. Anterior clypeal border concave. Mandibles with lateral carinae.

Mesosoma little convex in side view. Pronotum in dorsal view with the anterior border convex. Pronotal sides bearing broad lamellae; anterior border of the lamellae pointed, lateral border straight or gently concave, and the posterior one obtuse. Mesonotal teeth pointed. Propodeal suture variably impressed dorsally. Propodeum with differentiated basal and declivous faces; basal face often with a small denticle followed by a pointed, broad tooth and a thin, pointed spine longer than the face itself.

Petiole anteriorly truncate. Petiolar spines thin, pointed backwards and longer than the basal face of the propodeum. Petiolar dorsum with a faint transversal carina delimiting the anterior and posterior faces and medially with another longitudinal carina. Postpetiolar spines slightly curved distally. Postpetiolar dorsum with a longitudinal carina on the posterior half.

Gaster with a broad membranaceous anterior lamella, surpassing the first gastral stigma at least.

Fore femora broader than the hind ones. Hind and mid femora bidenticulate medially; mid and hind basitarsi laterally compressed.

Sculpture. Head dorsum, mesosoma and abdominal pedicel reticulate-punctate and densely foveolate. Ventral face of the head and propleurae reticulate-punctate, with superficial foveae and slightly rugulose. Lower face of the vertexal angles and dorsal third of the pleurae slightly shining. Declivous face of the propodeum, distal outer face and sides of the legs reticulate-punctate and with faint longitudinal rugosities.

First gastral tergite, ventral part of the meso- and metapleurae, distal outer face of the legs densely covered with small, oval, superficial foveae. First gastral sternite with few longitudinal, slightly anastomosing rugulae on its sides, the rest reticulate-punctate and slightly shining in the middle.

Pilosity. Head dorsum, mesosoma, pedicel, gaster, distal outer face of the femora and tibiae, ventral part of the meso- and metapleurae densely covered by canaliculate, appressed hairs. Ventral part of the head, propleurae, sides of the legs and first gastral sternite with the same hairs as above, but sparser. Legs with sparse, short, thick suberect hairs; similar hairs but longer on the apex of the gaster.

Colour. Black with the sides of the frontal carinae, the sides of the pronotal lamellae, the crest of the gaster, the masticatory margin of the mandibles, the apex of the propodeal and pedicular spines ferrugineous. Hairs golden.

Measurements (in mm) and indices: TL 5.46–6.44; HL 1.32–1.60; HW 1.68–2.04; EL 0.45–0.49; PW 1.60–1.88; PeW 1.28–1.68; PpW 0.96–1.20; HBaL 0.64–0.72; HBaW 0.2–0.24; CI 127.3–127.5; PI 105.0–108.5; PPeI 111.9–125.0; PPpI 156.6–166.7; HBaI 31.2.–33.3.

G y n e (Fig. 120) (previously undescribed). - Head subquadrate, convex and without disc. Frontal carinae broadly expanded anteriorly and straight posteriorly up to the posterior border of the eyes. Vertexal angles almost round, poorly angulate. Vertex with a pair of denticles. Mandibles with a lateral carina.

Mesosoma. Humeral angles with a broad, obtuse tooth. Pronotal carina marked in the middle and obsolete on the sides. Mesonotum and scutellum flat in side view. Lower mesopleurae with a denticle. Basal face of the propodeum laterally with two pairs of broad, pointed teeth, the posterior pair longer than the anterior one. Declivous face of the propodeum with posteriorly converging sides.

Petiole with distinct anterior and posterior faces; anterior face oblique; the posterior face declivous posteriorly and with a pointed spine directed backwards on the sides. Postpetiole

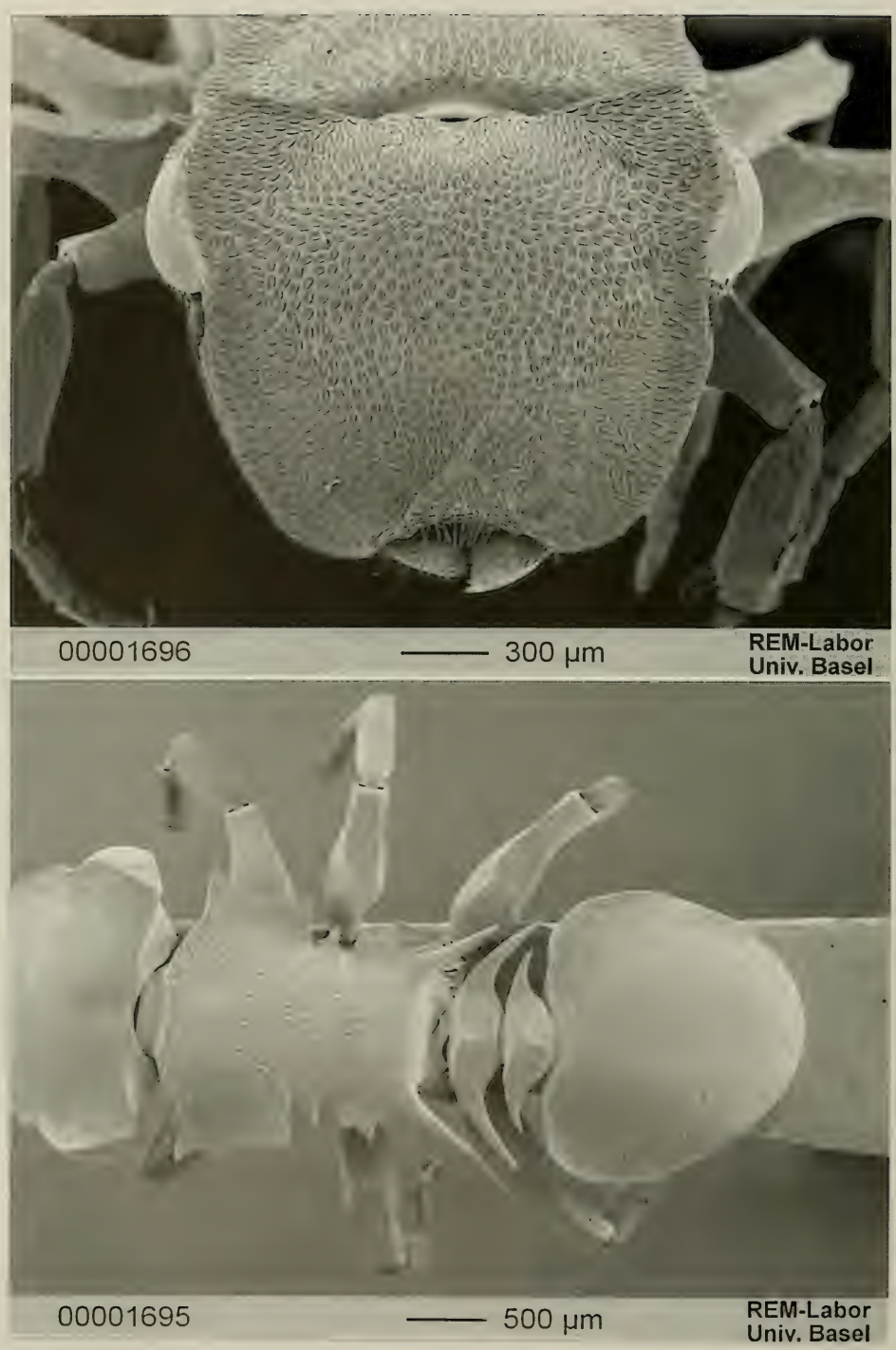


Fig. 119. *Cephalotes inca* (SANTSCHI). Worker from Grau (Tumbez), Peru: head (top) and meso- and metasoma (bottom) in dorsal view.

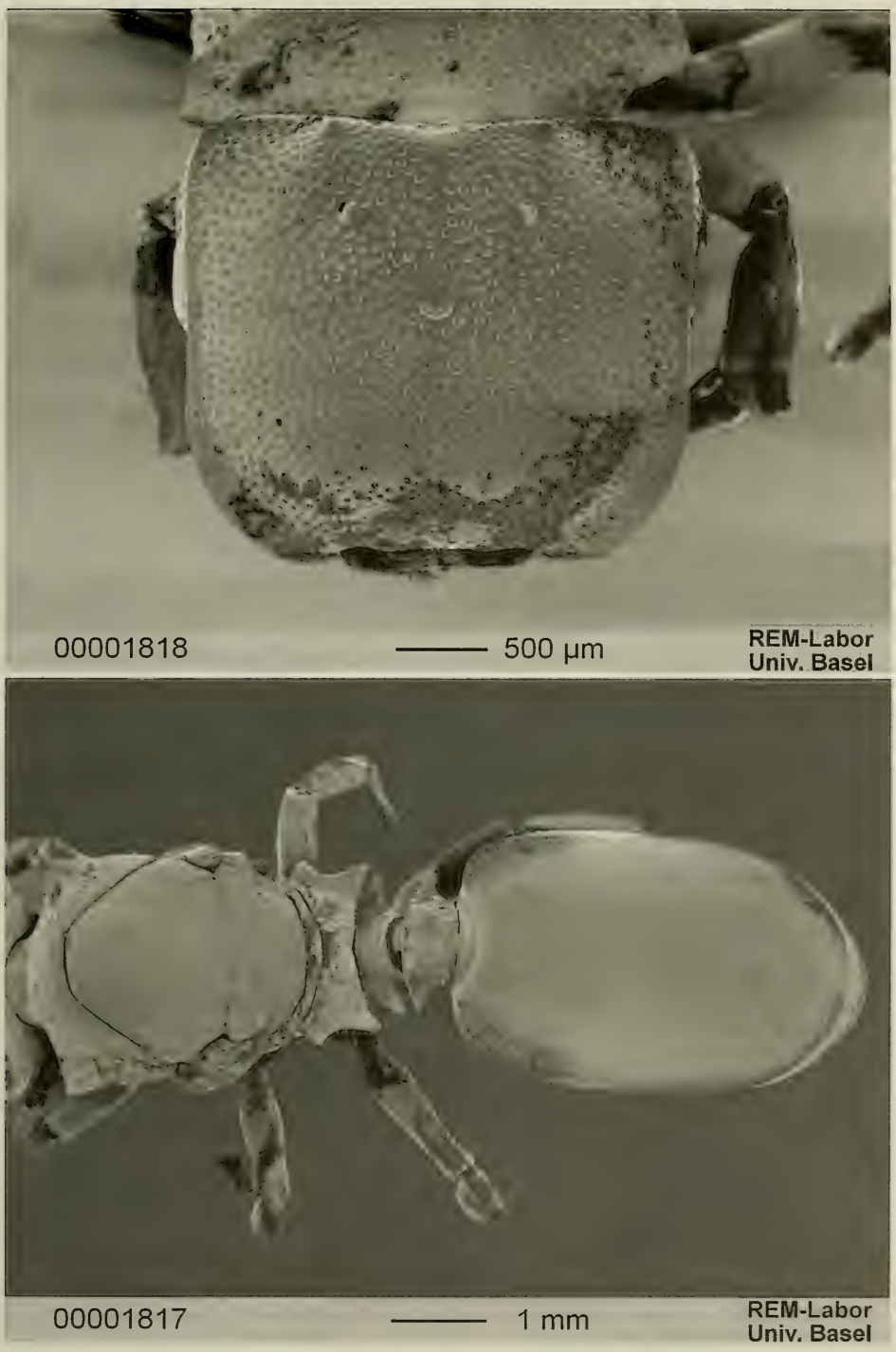


Fig. 120. *Cephalotes inca* (SANTSCHI). Gyne from Nanchoc Quebrada (Cajamarca), Peru: head (top) and meso- and metasoma (bottom) in dorsal view.

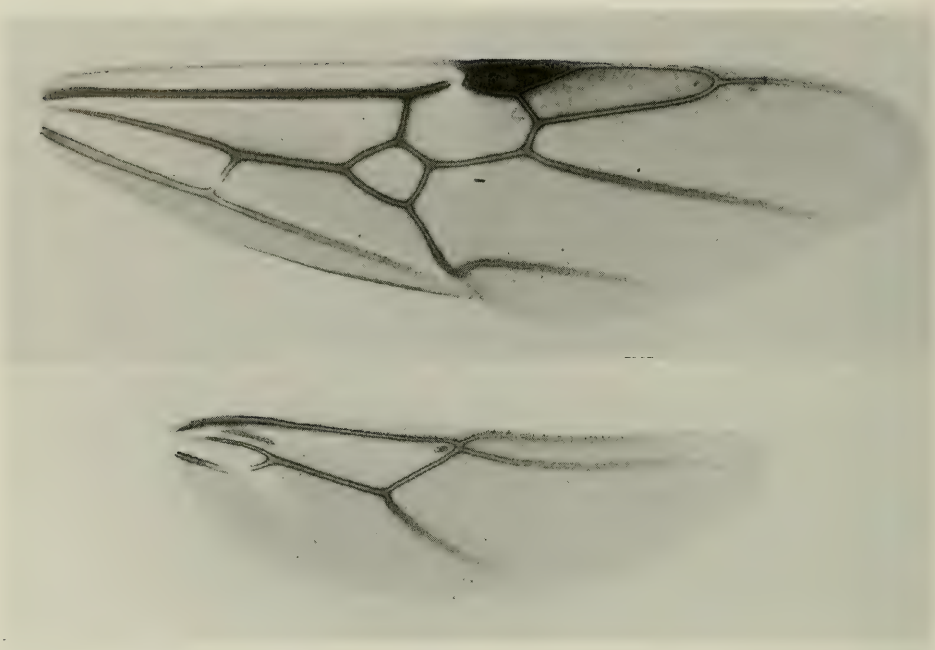


Fig. 121. *Cephalotes inca* (SANTSCHI). Gyne from Nanchoc Quebrada (Cajamarca), Peru, fore and hind wings.

broadly convex, with a strong incompletely "U" shaped dorsal carina; postpetiolar spines arising from the anterior border of the postpetiole and little curved.

Gaster marginate anteriorly by a narrow lamella.

Legs. Fore coxae with a tumulus anteriorly. Mid and hind femora angulate. Mid and hind basitarsi flat and broad at the base.

Wings as in Fig. 121.

Sculpture. Head, mesonotum, propodeum, pedicel and ventral part of the meso- and metapleurae superficially reticulate-punctate and covered by foveae broader than their interspaces, the foveae denser on the propodeum oval on the pedicel and meso- and metapleurae, sparse and large on the ventral part of the head. Declivous face of the propodeum, dorsal half of the metapleurae, femora, and tarsi superficially reticulate-punctate and shining. Anterior and posterior faces of the tibiae similarly sculptured with superimposed fine, longitudinal rugosities. Anterior and posterior fourths of the first gastral tergite, distal part of the outer face of the femora and outer face of the tibiae covered with dense oval foveae; the foveae sparser on the remaining tergites. Sternites superficially reticulate-punctate. almost shining, and with sparse superficial foveae.

Pilosity. Each fovea with an appressed, canaliculate hair of size proportional to the one of the foveae. Mandibles, mesosoma, pedicel and legs with rare, slightly clavate, suberect hairs. Second and remaining tergites and sternites with sparse, long, truncate hairs, rare on the first gastral tergite.

Colour. Black. Tip of the last funicular joints ferrugineous. Canaliculate hairs golden.

Measurements (in mm) and indices: TL 11.60–11.78; HL 2.44–2.48; HW 2.68–2.72; EL 0.62–0.64; PW 2.60–2.64; PeW 1.48–1.56; PpW 1.44–1.48; HBaL 0.88; HBaW 0.32; CI 108.1–111.5; PI 103.0–103.1; PPeI 160.0–175.7; PPpI 178.4–186.1; HBaI 36.4–36.6.

Material examined. - **Peru**: no further data, 1 gyne, MAGRETTI [MCSN]; La Masa, 400 m, 1906, 2 workers (syntypes) [NHMB], 1 worker (syntype) [MHNG], P. RIVET.

P i u r a : Piura, 1910, 1 worker, TOWNSEND [MCZC]. T u m b e z : Grau, 1 worker, G. A. BAER [MNHN]. C a j a m a r c a : Nanchoc Quebrada, 6°57´S, 79°15´W, 400 m, 21.XII.1984–17.I.1985, 1 gyne, J. M. CARPENTER [MCZC]. L a m b a y e q u e : Chiclayo, Hda. Patapo, 04.III.1963, 2 workers, R. PARDO [MZSP].

D i s c u s s i o n . - The two gynes from Peru tentatively identified by us as *inca* differ from the gyne of *basalis* by the absence of the pair of yellow spots on the first gastral tergite, by the much broader foveae on the head and by the weakly angulate vertexal angles.

C. inca shares with its closest relative, *basalis*, in the worker, the expanded pronotal lamellae with pointed anterior corner, the frontal carinae strongly upturned over the eyes, the vertexal angles triangular, the sides of the propodeum with a denticle (absent in some specimens) followed by a broad, pointed tooth and a long spine, and the long petiolar spines, and, in the gyne, the presence of a pair of vertexal denticles and the elongate propodeal and peduncular spines similar to those of the worker.

D i s t r i b u t i o n : Peru.

5.6.7. The *clypeatus* clade

A small (three species), very distinctive clade characterised by the following four synapomorphies: (1) vertexal angles of the worker triangular, (2) worker CI > 155, (3) worker pronotal spines fused with a lamella, (4) propodeal spines fused with a lamella. The triangular vertexal angles appear, homoplastically, also among workers of some of the species of the *basalis* clade. The high CI value, outside this clade, appears only in the basalmost species of the next closely related clade (the *multispinosus* clade): the Mexican fossil *C. poinari*. The three representatives of this clade had been formerly considered as a separate genus: *Zacryptocerus* s. str. If, on one hand, the synapomorphies listed above would be sufficient for the characterisation at generic level of these three species, such a decision is rendered impossible by the examination of our cladogram since it would render paraphyletic any other generic distinction of its most related species.

Species included in the clade: *clypeatus*, *membranaceus*, *ustus*.

Cephalotes ustus (KEMPF) new combination
Fig. 122

Zacryptocerus ustus KEMPF, 1973: 450, figs. 1, 4. Worker. Original description. Type locality: Pedra Azul, 800 m (Minas Gerais, Brazil). Type material: Holotype and paratype workers labelled: "Pedra Azul – MG, 800 m, XI–1972, Seabra & Alvarenga, no. 8816, Holotypus and Paratypus", in MZSP, examined.

D i a g n o s i s . - A member of the *clypeatus* clade characterised in the worker and in the soldier by the dark brown body, by the head, mesosoma, pedicel and gaster surrounded by a yellow-whitish, opaque lamella, and by the strong body sculpture.

W o r k e r (Fig. 122) (description by KEMPF, 1973). - "Total length 7.7 (6.9) mm; maximum head length 2.08 (2.79) mm; maximum diameter of eyes 0.38 (0.37) mm; Weber's length of thorax 2.24 (2.00) mm; maximum width of thorax across pronotum 2.87 (2.71) mm. Deeply fuscous brown, almost black; gaster and tarsomeres black; membranaceous laminate borders of head, thorax, gaster and spines of petiole and postpetiole testaceous. Integument opaque, finely, densely punctulate, including the laminate borders which are not glassy nor hyaline. Dorsum of head, cheeks, dorsum of thorax, of petiole, postpetiole and gaster, apical

half of extensor face of femora, tibiae densely and shallowly foveolate, each foveola being oblong and containing an appressed, canaliculate, golden hair. The same hairs are much more widely scattered, either canaliculate or simple, on gular surface of head, sides of thorax, sides of femora and tibiae, ventral surface of gaster, with the foveolae usually indistinct. Gaster, in addition, very finely reticulate-rugulose. Standing hairs absent.

Head distinctly transverse, sides slightly diverging caudad, occipital angle spinous, acute, the spine with a laterally projecting lobe, smaller yet similar to that of *membranaceus*. Frontal carinae and occipital borders membranaceous and somewhat upturned. Dorsum of head gently convex on disc in both directions, laterally transversely concave. Clypeal sutures vestigial. Frontal area obsolete. Cheeks immarginate below. Eye stalk entirely fused to the frontal carinae above, the apical part bearing the eye not free. Eyes relatively larger, their maximum diameter equal to the distance between their posterior orbit and the tip of the occipital spine. Thorax as in *membranaceus* except for the different sculpture already mentioned above; lateral expansions of the pronotum scarcely raised apicad, horizontal, those of propodeum obliquely upturned. Hind femora marginate above on apical half yet not sharply carinate, angulate above in side-view, the angle situated beyond the first third of the femur length. First tarsomere distinctly yet not strikingly longer than tarsomeres 2–5 combined. Petiole, postpetiole and gaster as in *membranaceus* except for the differences in sculpture, color and pilosity already mentioned above".

Measurements (in mm) and indices: TL 6.44–7.28; HL 1.52–1.68; HW 2.40–2.68; EL 0.37; PW 2.56–2.80; PeW 0.92–1.02; PpW 0.88–1.00; HBaL 0.72–0.76; HBaW 0.25–0.27; CI 157.9–163.4; PI 93.7–97.7; PPeI 270.6–283.3; PPpI 276.0–309.1; HBaI 34.7–37.5.

S o l d i e r (previously undescribed). - Head feebly convex. Frontal carinae convex anteriorly; their sides slightly converging over the eyes and continuing to the vertexal angles; the latter in form of broad, pointed teeth interconnected by a broad lamella interrupted in the middle. Vertex with a pair of median teeth equally connected by a carina. Mandibles broad, with a strong lateral carina.

Mesosoma. Pronotal sides with a broad lamella, with convex anterior border and posteriorly converging sides. Pronotal carina wide, superficially interrupted in the middle; its sides forming an obtuse tooth in the middle of the notopleural angle. Promesonotal suture impressed on the sides. Mesonotum with a broad, obtuse tooth. Propodeal suture deeply impressed. Propodeum bearing a pair of long spines round at the apex, its basal and declivous face clearly differentiated. Basal face of propodeum with a broad lamellaceous border with 1–2 denticles anteriorly followed by a round tooth and embedding laterally the propodeal spines. Dorsum of propodeal spines markedly carinated.

Petiole with the anterior border truncate and slightly concave medially; posterior face of the petiole flat. Petiolar spines with lamellaceous round tips directed backwards. Postpetiolar spines as in the petiole, originating from the anterior face of the postpetiole and curved laterally.

Legs. Fore coxae with a pointed anterior spine. Mid and hind femora forming an angle without denticles. Hind basitarsi flat and broad at the base.

Gaster oval and surrounded by a broad lamellae with a notch on its posterior middle.

Sculpture. Head, mesosoma and pedicel punctate and covered by foveae sparser and shallower on the middle of the frontal carinae and on the meso- and metapleurae. Ventral face of the head with broader foveae than those on the head dorsum; similar foveae but sparser on the propleurae. Posterior half of the declivous face of the propodeum, dorsal half of the metapleura, legs and gaster reticulate-punctate, with faint foveae and anastomosing rugosities on first gastral tergite. Middle of the first gastral sternite shining, with sparse piligerous punctures. Membranaceous border surrounding the body reticulate-punctate.

Pilosity. Each fovea bearing an appressed, canaliculate hair of size proportional to the one of the fovea; gaster covered by dense hairs as on the head. Legs with the same type of hairs as the gaster, but sparser. Thin, sparse, appressed hairs on the legs and on the middle of the first gastral sternite. Apex of the gaster with sparse, long, thick, erect hairs truncate or pointed.

Colour. Dark brown to black. Frontal carinae and vertexal angles yellowish-brown, lamellae of the mesosoma, of the pedicel and of the gaster lighter.

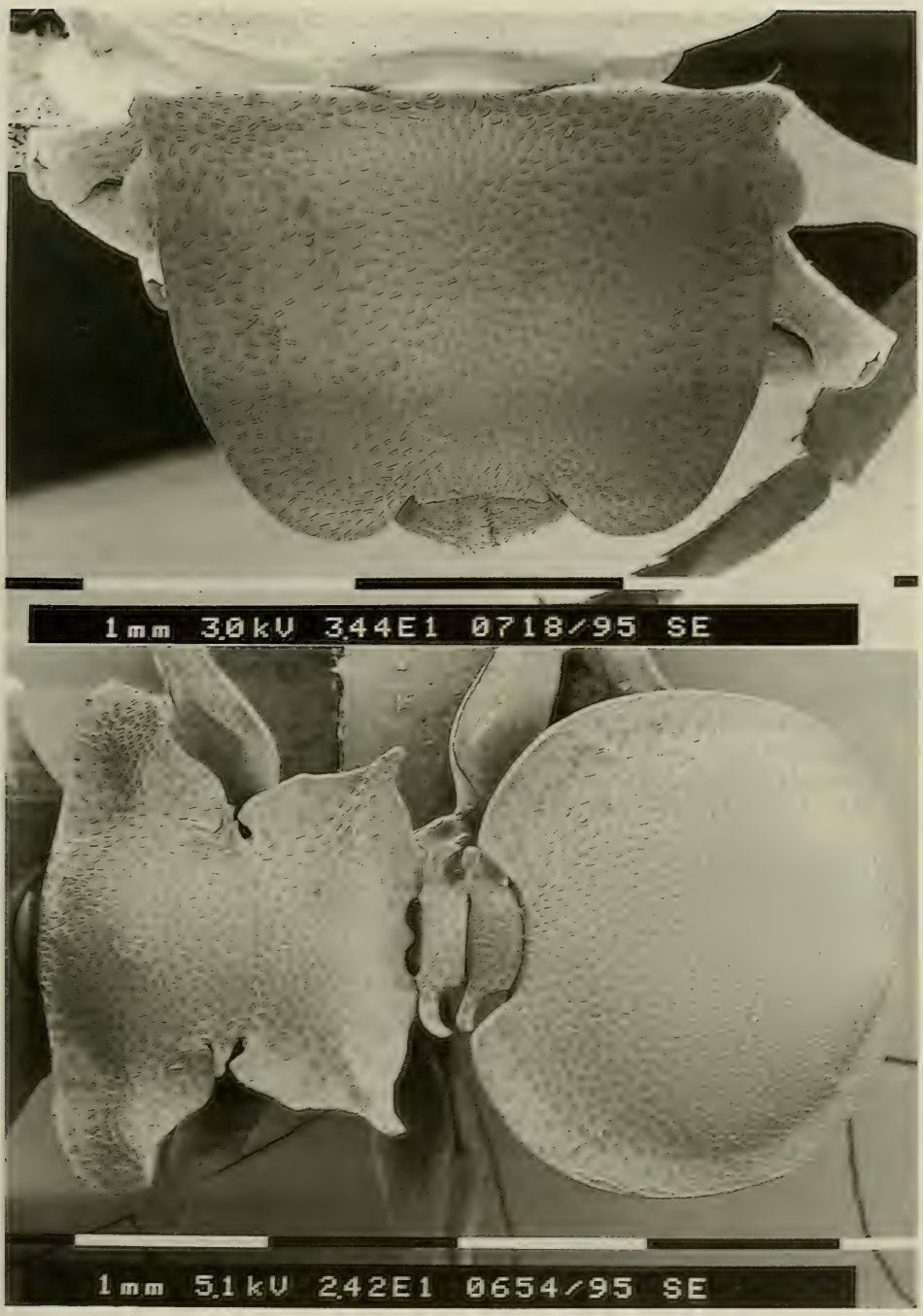


Fig. 122. *Cephalotes ustus* (KEMPF). Worker from Maracás (Bahia), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 8.84–8.88; HL 2.12–2.16; HW 2.92–3.00; EL 0.44; PW 3.16; PeW 1.16; PpW 1.08–1.12; HBaL 0.88–0.92; HBaW 0.30; CI 137.7–138.9; PI 92.4–94.9; PPeI 272.4; PPpI 282.1–292.6; HBaI 32.6–34.1.

Material examined. - **Brazil**: Bahia: Encruzilhada, 980 m, XI.1973–1974, 13 workers, C. A. C. SEABRA & M. ALVARENGA [MZSP]; Vitória da Conquista, 28.I.1994, 3 workers, J. H. C. DELABIE [CPCC, USNM]. Minas Gerais: Pedra Azul, 800 m, XI.1972, 2 workers (holotype and paratype), C. A. C. SEABRA & M. ALVARENGA [MZSP]; Maracás, Fazenda Maria Inácia, Mata Cipó, 24–29.XI.1990, 35 workers, 3 soldiers, C. R. F. BRANDÃO, J. M. DINIZ & P. S. OLIVEIRA [MZSP].

Discussion. - The distinction of this species from the other two members of the clade emphasised by KEMPF (1973), based on workers only, is not supported by the first discovery of the soldier. *Ustus*, in our analysis, still results as outgroup of both *clypeatus* and *membranaceus* essentially by the possession of the plesiomorphic morphology of the propodeal spines (straight instead of curved forward as in the other two species of the clade).

Distribution: Brazil.

Cephalotes clypeatus (FABRICIUS)
Figs. 123, 124, 125, 382

Cryptocerus clypeatus FABRICIUS, 1804: 420. Worker. Original description. Type locality: "in America meridionali", actually Essequibo, Guyana. Type material: 2 syntype workers in the ZMUC and 2 syntype workers belonging to the Zoologisches Museum Kiel equally deposited in ZMUC (ZIMSEN, 1964: 427) (examined). Only one of the ZMUC syntypes bears a locality label:" Essequibo, Smidt, Mus. de Sehestedt, *Cryptocerus clypeatus* Fabr."

Cryptocerus clypeatus FABRICIUS, SMITH, 1854: 217, pl. 21 figs. 1, 2, 5, 6. Gyne, male.

Cephalotes clypeatus FABRICIUS, EMERY, 1914: 39. First combination in *Cephalotes*.

Cryptocerus clypeatus FABRICIUS, FOREL, 1923, Pl. I, fig. a. Soldier, gyne, male (colour figure).

Zacryptocerus clypeatus (FABRICIUS), WHEELER, 1911: 175. First combination in *Zacryptocerus*.

Zacryptocerus clypeatus (FABRICIUS), KEMPF, 1951: 136, figs. 105, 109, 111. Worker, gyne, male.

Zacryptocerus clypeatus (FABRICIUS), KEMPF, 1973: 456, figs. 3, 7. Soldier.

Zacryptocerus clypeatus, JAFFE C., 1993: pl. 18. Worker (colour figure).

Diagnosis. - A member of the *clypeatus* clade characterised in the worker and in the soldier by the body shining yellowish to light brown with the head, mesosoma, pedicel and gaster surrounded by a transparent lamella, and, in the soldier, by the vertexal angles with a pointed spine, and, in the gyne, by two pairs of whitish spots surrounded by a dark border on the gaster.

Worker (Fig. 123) (description of KEMPF, 1951). - "Length 6.5 – 10.0 mm. Ochraceous to yellowish brown. Head, thorax and gaster fulgid, sparsely covered with small, shallow foveolae, each containing a minute decumbent, scale-like hair. Head transverse, broader than long. Mandibles densely punctate-rugulose, fulgid. Clypeus triangular, its anterior border emarginate, the sides converging behind, the sutures visible. Frontal area small, vestigial. Frontal carinae diverging behind, somewhat upturned laterad, subtranslucid, slightly more pigmented, sculptured and subopaque along the margin. Occipital corners subspinose, acute. Occipital border crested, more or less sinuate. Eye-stalk fused above with the frontal carinae; eyes small. Cheeks immarginate below. Upper surface of thorax, except the expanded laminate and translucid border, more or less flat. Anterior border of pronotum more or less straight, with a narrow subhyaline crest. Scapular spine long, upturned, and recurved distad,

contained within a broadly expanded subhyaline border. Transverse pronotal crest absent, except a median single denticule. Promesonotal suture absent. Mesonotum with a lateral membranaceous, slightly upturned subhyaline tooth. Mesoepinotal suture present. Epinotum not distinctly divided into a basal and declivous face, moderately convex, its sides expanded into a broad, rounded somewhat upturned subhyaline border, containing a few pigmented strands representing the vestiges of the epinotal spines. Femora moderately incrassated at the proximal third, attenuate distad. Basitarsi of mid and hind legs compressed, yet not as thin as in *Cephalotes*. Both the tibiae and the basitarsi have elongate, dense grooves, containing a decumbent hair. Petiole more than twice as broad as long, with an anterolateral, slightly recurved tooth, the anterior border marginate, the ventral face with a hyaline median tooth. Postpetiole broader, with a lateral, plate-like, apically rounded lobe, curving forward. Gaster oval, depressed, surrounded by a narrow, hyaline, upturned, translucid border, interrupted mesally in front for the reception of the postpetiole."

Measurements (in mm) and indices: TL 7.20–8.96; HL 1.76–2.12; HW 2.88–3.16; EL 0.32–0.39; PW 2.80–3.48; PeW 0.88–1.00; PpW 0.88–0.96; HBaL 1.10–1.24; HBaW 0.28–0.31; CI 162.5–172.7; PI 90.8–108.6; PPeI 304.3–348.0; PPpI 327.3–362.5; HBaI 23.3–25.4.

S o l d i e r (description of KEMPF, 1973). - "This caste has the cephalic disc with the sides less diverging caudad, its surface more distinctly and densely foveolate; the vertex bears a pair of teeth at the bases of which are connected by a low transverse carina, which is however lacking between each tooth and the lateral margin of head. Pronotum with a well-developed transverse carina, the anterior and posterior portion of thorax forming in side view a blunt angle the vertex of which is the carina. Propodeal spines well-developed, solid and stout with the enclosing hyaline margin. Intermediates seem to be more frequent and differ from the minor worker only by the presence of a pair of unconnected teeth on vertex, a weak, often incomplete transverse pronotal carina, and the solid spine within the lateral propodeal margin".

Measurements (in mm) and indices: TL 10.05–11.24; HL 2.48–2.60; HW 3.64–3.84; EL 0.42–0.44; PW 3.88–4.16; PeW 1.16- 1.20; PpW 1.10–1.16; HBaL 1.28–1.32; HBaW 0.32–0.34; CI 146.7–147.7; PI 92.3–93.8; PPeI 334.5–346.6; PPpI 352.7–358.6; HBaI 24.2–26.5.

G y n e (Fig. 382) (description of KEMPF, 1951). - "Length 13 mm. Median head length 2.53 mm; Weber's length of thorax 4.05 mm. Ochraceous; the following ferruginous: Antennae, tarsi, mandibles. First gastral tergite with a pale yellowish macula, surrounded by a fuscous ring, open towards the outer margin, on each corner. Parts of the frontal carinae and crests of the pronotum are subhyaline and semitranslucid.

Head subfulgid above, subopaque below; subquadrate. Mandibles visible from above, finely rugulose, sparsely punctured, the apices curved obliquely downward. Clypeus retracted, subtriangular, anterior border emarginate. Frontal area vestigial. Frontal carinae greatly expanded, covering the sides of the head from above, extending backwards to the occipital corner; semitransparent, laterally straight, upturned, rounded anteriorly. Upper surface of head slightly concave discad, microscopically and rather sparsely punctured, covered with large, sparse, rounded foveolae, each containing a small, whitish, decumbent scale. Ocelli forming an equilateral triangle, situated on large pits, on the side walls. Behind the posterior ocelli two short, stout, acute spines.

Occipital angle with a similar spine, its base continuous with frontal carinae and sending out a crest, downwards and mesad toward the occipital foramen, fading out shortly before reaching it. A sharp crest separating the cheek from the lower surface of the head. Scape attenuate at base, incrassated discad. Eyes situated behind the antennal scrobe.

Thorax fulgid, one and a half times as long as broad; sparsely foveolate, each foveola containing a decumbent seta. Anterior border of pronotum scarcely emarginated mesad, slightly crested. Shoulders with a large, angular, protruding crest, marginating the sides until it gives off, on each side, the transverse pronotal crest, the remaining part of the lateral border of the pronotum immarginate. Laterotergite of pronotum flat. Mesonotal sclerites flat. Parapsidal furrows of scutum vestigial. Scutum almost twice as broad as long. Mesopleura

Fig. 123. *Cephalotes clypeatus* (FABRICIUS). Worker from Lins (São Paulo), Brazil, general habitus.

convex, the lower half without an antero-ventral tooth. Basal face of epinotum extremely short, mesad, marginate and crested laterad, forming an acute, crested angle caudad, where the crest turns mesad, for one fourth of the width. Declivous face almost three times as long as basal face, somewhat excavated. Mid and hind basitarsus broadened and flattened, almost as in the female *Cephalotes*. Femora, tibiae and tarsi with elongate, decumbent long hair.

Petiole twice as broad as long, impressed above, mesad, its anterior border slightly emarginate. Densely foveolate above and laterad, sides slightly converging caudad. Anterior half of the ventral face with a median crest, ending in an acute tooth anteriorly. Postpetiole more than twice as broad as long, with an anterolateral, projecting blunt, marginate and crested lobe, the dorsal face greatly convex above longitudinally and transversely, sculptured as petiole.

Gaster fulgid, elongate, suboval, sides subparallel. Anterior corners not crested, but lobate, immarginate. Both the tergites and sternites are very finely and shallowly foveolate except on the posterior border of the sclerites where the foveolae become crowded and the integument rugulose.

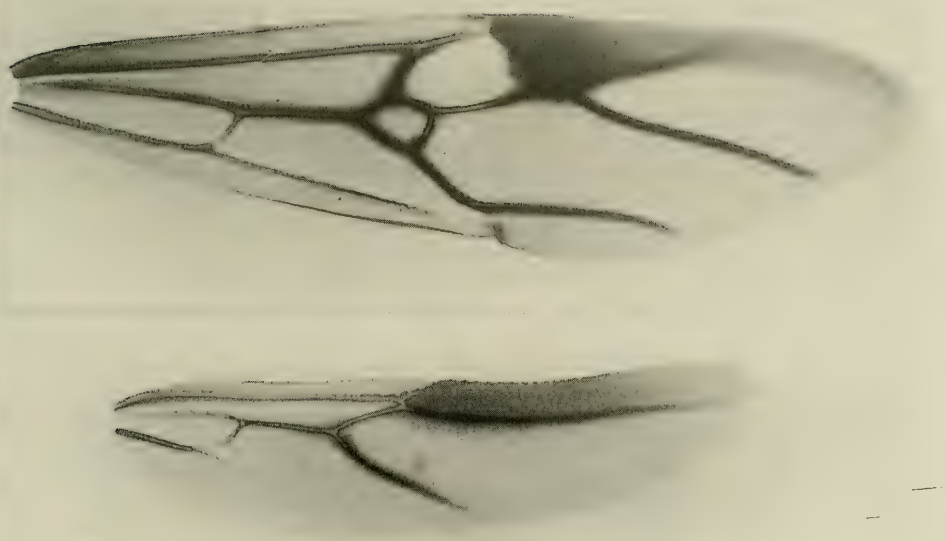


Fig. 124. *Cephalotes clypeatus* (FABRICIUS). Gyne from Lins (São Paulo), Brazil, fore and hind wings.

Wings subhyaline. Veins dark brunneous. Fore wing with a black stigma. Marginal cell infuscated, closed, appendiculate, narrow, and elongate. Submarginal cell elongate, its apical half infuscated. A fuscous streak along the veins in the apical field and in the costal margin. No transverse cubital vein. Discoidal cell small".

Wings as in Fig. 124.

Measurements (in mm) and indices: TL 13.40–14.10 HL 2.56–2.60; HW 2.88–3.08; EL 0.48; PW 2.92–3.20; PeW 1.00–1.16; PpW 1.20–1.28; HBaL 1.32–1.36; HBaW 0.35–0.39; CI 112.5–118.4; PI 96.2–98.6 PPeI 275.8–292.0; PPpI 243.3–250.0; HBaI 26.5- 28.7.

M a l e (description of KEMPF, 1951). - "Length 8.4 mm. Median head length 1.26 mm; Weber's length of thorax 2.80 mm. Black; the following stramineous: Mandibles, antennae, legs, excluding the coxae, gaster. Brunneous: clypeus, a central patch discad on each of the three parts of the scutum, metanotum, edges of lateral sclerites of thorax, fore coxae, peduncle; the postpetiole ferruginous.

Head subopaque, transverse, median head length shorter than distance between the eyes. Mandibles finely ruguloso-punctate, with a longitudinal crest basad. Chewing border finely crenulate with a distinct apical and minute preapical tooth. Clypeus transverse, evenly convex, not forming two faces, anterior and posterior border arcuate. Frontal carinae raised to a conspicuous triangular acute tooth between the antennal sockets, diverging behind, fading out before the posterior half of the eyes. Front finely punctate-rugulose. Antennal scrobe obsolete. Cheeks, vertex, occiput and lower surface of head more coarsely reticulate-rugose, interspersed with larger setigerous foveolae. Ocelli on vertex, large, raised above the surface of the head, the lateral ones larger than the antero-median ocellus. Occiput perpendicular to

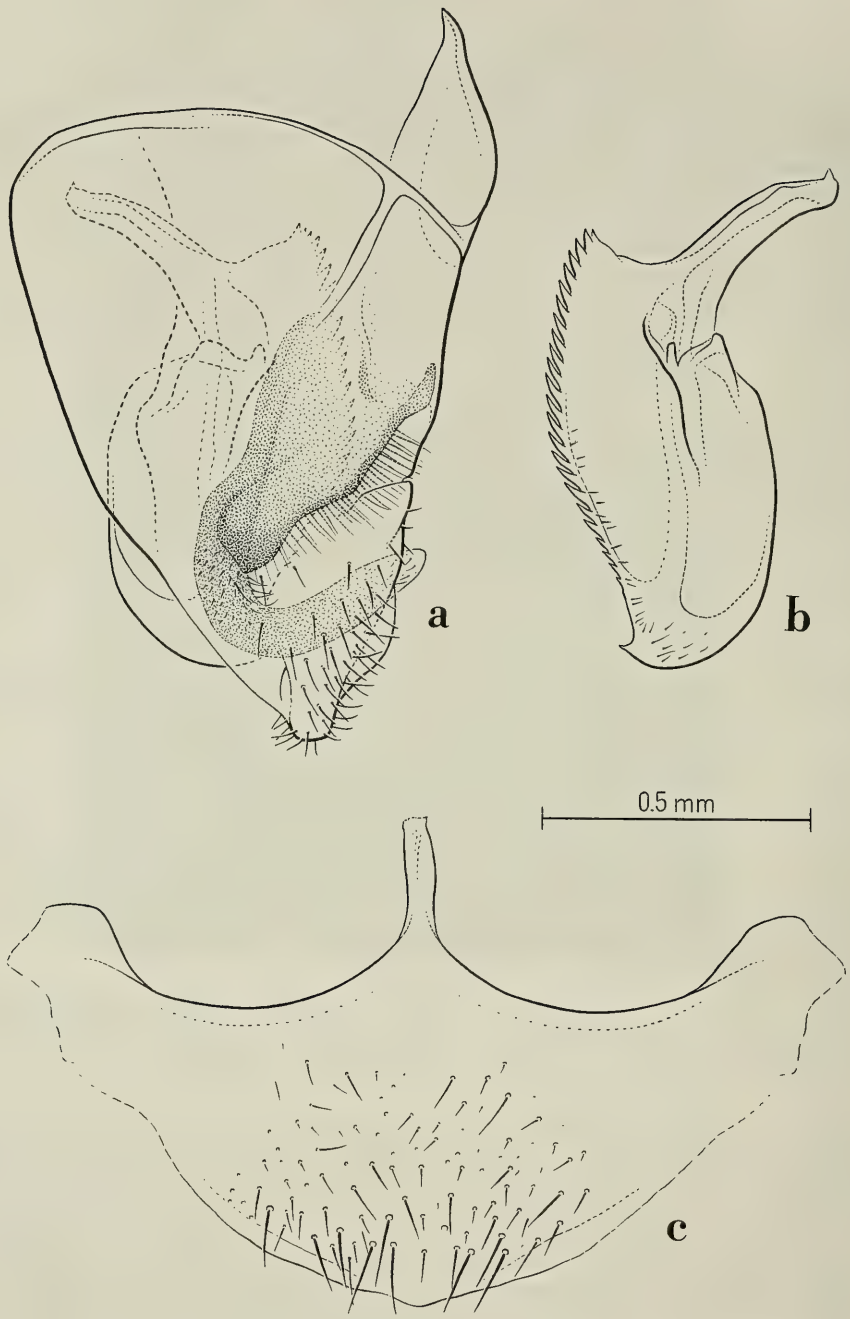


Fig. 125. *Cephalotes clypeatus* (FABRICIUS). Male from Lins (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

the upper surface of head, immarginate above, slightly excavated beneath mesad, occipital angles obsolete. Cheeks, in anterior aspect, diverging caudad, subcontinuous with the anterior border of the mandibles, scarcely emarginate. Eyes large, slightly shorter than half the median head length. Scape shorter than half the length of the 2nd funicular segment. Segments 2–12 of funiculus more than twice as long as broad.

Thorax subfulgid; 1.5 times as long as maximum width. Anterior border of pronotum moderately arcuate, with bluntly angulate, projecting shoulder. Median portion of the dorsal face and the laterotergite of the pronotum mostly smooth and fulgid, the postero-lateral portions of the above rather coarsely foveolate-rugose. Scutum smooth and fulgid, sparsely and shallowly foveolate, the Mayrian furrows not fusing mesad behind. Scutellum similarly sculptured, the anterolateral lobes separated from the body by a very deep transverse furrow. Metanotum subopaque. Upper and lower portion of metapleura greatly convex and bulging. Epinotum unarmed, densely foveolate above, rather smooth and fulgid laterad and on the declivous face. Mid and hind basitarsi flattened basad. Legs fulgid. Claws stout, with a blunt basal tooth.

Petiole subquadrate from above. Upper surface smooth and fulgid, sides scarcely converging caudad, with a few scattered foveolae below. Pospetiole slightly broader than long, with a blunt tubercle projecting from each side. Upper face convex in profile. Sculpture as petiole.

Gaster oval, perfulgid. Exposed portions of tergites 2–6 with very fine, inconspicuous microsculpture. (The genitalia were lost).

Pilosity long, pale creamy, sparser than in *Cephalotes*. Erect on head and thorax, appressed on appendages.

Wings as in female".

Genitalia and subgenital plate as in Fig. 125.

Measurements (in mm) and indices: TL 7.00–8.68; HL 1.08–1.28; HW 1.32–1.60; EL 0.41–0.52; PW 1.46–1.84; PeW 0.66–0.76; PpW 0.73–0.84; HBaL 0.78–0.96; HBaW 0.15–0.20; CI 122.2–125.0; PI 86.9–90.4; PPeI 221.2–242.1; PPpI 200.0–219.0; HBaI 19.2–20.8.

Material examined. - **Colombia**: Cundinamarca: Nova Granada (= Santafé de Bogotá), 2 workers [MHNG, MCSN]. Amazonas: Leticia, 50 m 30.IX.1973, 1 worker, M. L. Corn [MZSP]; Leticia, Aug. 1974, 2 workers, M. L. Corn [MZSP].

Venezuela: San Esteban, III.88, 2 workers, E. Simon [MCSN]. Amazonas: Orinoco Delta, 12.II.1935, 34 workers N. A. Weber [MCZC]; P. Anduze, Nov.1940, 1 worker [MCZC]. Monagas: Las Vegas, Mundo Nuevo, 650 m, 18.IV.1978, 1 worker, C. Bordon [MCZC]. Nueva Esparta: Pampatar, Isla Margarita, 27.II.1982, 1 worker, C. R. F. Brandão, L. Campos & K. Tickmann [MZSP].

Trinidad & Tobago: Trinidad: no further locality, 9 workers, Urich [MHNG]; no further locality, 09.IV.1935, 1 worker, N. A. Weber [MCZC]; St. Augustine, B. W. I., 22.V.1936, 1 worker, N. A. Weber [MCZC]. Saint George: Maracas Valley, B. W. I., 23.III.1935, 1 worker, N. A. Weber [MCZC]; Port of Spain, 2 workers [MZSP]. Nariva: near Río Claro, B. W. I., 01.VI.1936, 1 worker, 1 gyne, N. A. Weber [MCZC]. Saint Andrew: Sangre Grande, 2 workers, R. Thaxter [MCZC]. Mayaro: Mayaro Bay, B. W. I., 1 worker, N. A. Weber [MCZC]. Tobago: no further locality, 13–15.VII.1962, 10 workers, J. Maldonado [USNM].

Guyana: Berbice: Co. Rosignol, 0–5 m, 14.VII.1987, 1 worker, S. H. McKamey [USNM]; Demerara: Georgetown, 19.VI.1927, 3 workers [MCZC]; Mon Repos, 1975, 6 workers, B. K. Rai [MZSP]. Essequibo: no further locality, 4 workers (syntypes), Smidt [ZMUC]; Upper Rupununí, Fev. -Mar., 1 worker, Ozilno [MCZC].

Brazil: no further locality, 1 gyne [MHNG]; no further locality, 6 workers, Kulhorn [ZSMC]. Roraima: Alto Paraíso, 26.1X–0 2.XI.1985, 5 workers, MZ-Polonoroeste [MZSP]; Tapera, 3 workers, B. Pickel [MZSP]; Santa Cruz da Serra, 04–10.XI.1985, 2 workers, MZ-Polonoroeste [MZSP]. Amapá: Curiaú, 23.VXI.1991, 2 workers, Gorayeb [MPEG]; Amazonas: without further locality, 5 workers, 1 gyne, H. W. Bates [ZSMC]; Itacoatiara, 1 worker, 1 gyne, Mann & Baker [MCZC]; Manaus, centro da cidade,

13.I.1933, 2 workers, A. PACÍFICO [MZSP]; Manaus, 1 worker, ROMAN [MCZC]; Lago do Rei, Ilha do Careiro, 12.IV.1967, 1 worker, Exp. Perm. Amaz. [MZSP]; Tefé (Egas), second trimestre of 1879, 1 worker, M. DE MATHAN [MCSN]. P a r á : Conceicão do Araguaia, 17–21.XI.1979, 2 workers, W. L. OVERAL & W. FRANÇA [MPEG]; Left side of the Tucuruí, 12–16.III.1979, 2 workers, W. L. OVERAL [MPEG]; Ponta de Pedras, 6.III.1979, 7 workers, W. FRANÇA [MPEG]; Serra Cipó Pitanga, Baixo Rio Xingú, 30.XI.1983, 5 workers, B. MASCARENHAS [MPEG]; Utinga, 12.X.1979, 6 workers, F. F. RAMOS [MPEG]; Estr. Oriximiná, Óbidos, 28.I.1968, 1 worker, Exp. Perm. Amaz. [MZSP]; Óbidos, 42 workers [MHNG]; Santarém, Fazenda Taperinha, II. 1968, 24 workers, Exp. Perm. Amaz. [MZSP]; Santarém, Taperinha, 11–20.VI.1927, 1 worker, B. FINZI [MCZC]. M a r a n h ã o : Açailândia, P. Maranhão, 24.IX.1986, 1 worker, B. MASCARENHAS [MPEG]. P i a u í : Matias Olimpio (Fronteira com MA), 27.I.1976, 18 workers, A. J. CARDOSO & A. PRADO PIRES [MZSP]; 5 km E Oeiras, Fazenda Talhada, 13–17.XI.1991, 32 workers, 4 soldiers, C. R. F. BRANDÃO & P. MOUTINHO [MZSP]; 10 km N of Corrente, Fazenda Maracujá, 23–27.XI.1991, 7 workers, C. R. F. BRANDÃO [MZSP]. P e r n a m b u c o : Recife, 1938, 7 workers, L. LIMA CASTRO [MZSP]. A c r e : Cruzeiro do Sul, Dec. 1959, 1 worker, P. L. HERBST [MZSP]; Rio Branco, 1972, 2 workers, L. TRAVASSOS [MZSP]. R o n d ô n i a : Ig. Marmelo, Rio Abunã, Nov. 1962, 1 worker, Werner BOKERMANN [MZSP]; Porto Velho, Rio Madeira, 9 workers, MANN & BAKER [MCZC]. G o i á s : without further locality, 19.V.1906, 3 workers, BAER [MZSP]; Tras. Paul., 2 workers [MZSP]; Campinas, Nov. 1927, 1 gyne, SCHWARZMEIER [MZSP]; Campinas, 17.VII.1928, 2 workers, SCHWARZMEIER [MZSP]; Ilha do Bananal, 1 worker, 1 male, H. HIMMELREICH [MZSP]; Jataí, I 1955, 1 worker, M. CARREIRA [MZSP]; Jataí, Fazenda Aceiro, 2 workers [MZSP]; Jataí, Nov. 1972, 1 worker, F. M. OLIVEIRA [MZSP]; Santa Rita de Paranaíba, Jul. 1926, 2 workers, SCHWARZMEIER [MZSP]. B a h i a : Camisão, 1925, 3 workers, G. BONDAR [MZSP]; Itaberaba, Fazenda Riacho do Uruçu, 01–05.XII.1990, 45 workers, 1 gyne, C. R. F. BRANDÃO, J. M. DINIZ & P. S. OLIVEIRA [MZSP]; Castro Alves, 20.II.1994, 1 soldier, 1 gyne, 1 male, O. MARQUES [CPCC]. M a t o G r o s s o : without further locality, Nov. 1961, 28 workers, F. M. OLIVEIRA [MZSP]; Cáceres (different from Cáceres in Mato Grosso do Sul), 15–18.X.1961, 12 workers, F. M. OLIVEIRA [MZSP]; Cuiabá, 04.XII.1984, 9 workers, J. C. TRAGER [MZSP]; Chapada dos Guimarães, 10.II.1976, 1 worker, R. L. ARAÚJO [MZSP]; Chapada, May 1959, 1 worker, F. CANUTO [MZSP]; Poconé, 04.VI.1972, 2 workers, 22.IV.1973, 3 workers, R. N. WILLIAMS [MZSP]; Rio Sacre, 06.VIII.1961, 1 worker, K. LENKO [MZSP]; Utiariti, Rio Papagaio, 30.X.1966, 26 workers, LENKO & PEREIRA [MZSP]; Utiariti, 325 m, Rio Papagaio, Jul. Aug. 1961, 18 workers, K. LENKO [MZSP]; Xingu, Nov. 1961, 1 worker, ALVARENGA & WERNER [MZSP]. M a t o G r o s s o d o S u l : BR 262, km 457, 10.X.1989, 4 workers, B. H. DIETZ [SMNS]; Coxim, Taquaresinha, 10–20.X.1963, 1 soldier, V. C. A. CUNHA [MZSP]; Dourados, Colônia Vicentina, I.1962, 1 gyne, R. MUELLER [MZSP]; Ilha de Taiamã, Rio Paraguai, 10.VIII.1980, 10 workers, C. R. F. BRANDÃO [MZSP]; Murtinho (= Porto Murtinho?), Nov. 1927, 1 worker, MELZER [MZSP]; Fazenda Murtinho, I. 1930, 2 workers, SPITZ [MZSP]; Rio Baía, Nov. 1959, 1 worker, O. P. FORATTINI [MZSP]; S. João do Paranaíba, Fazenda Fortaleza, Córrego Barreiro, 29.III–13.VII.1972, 6 workers, J. M. DINIZ [MZSP]; Salobra (= rio Salobra?), Jul. 1939, 1 worker [MZSP]; Três Lagoas, 16.IX.1964, 8 workers [MZSP]; Barragem da Ilha, Três Lagoas, Nov. 1964, 14 workers, Exp. Depto. de Zoologia [MZSP]; Três Lagoas, Fazenda Beija Flôr, 22.VI.1964, 28 workers, Exp. Depto. Zool. [MZSP]; Três Lagoas, Fazenda do Cervo, 15–18.IX.1964, 14 workers, Exp. Depto. Zool. [MZSP]; Três Lagoas, Fazenda Canaã, Nov. 1966, 2 workers, F. LANE [MZSP]; Três Lagoas, Fazenda Dr. José Mendes, 15.V.–16.VI.1964, 22 workers, Exp. Depto. Zool. [MZSP]. M i n a s G e r a i s : Cana Brava, Rio Uberaba, May. 1966, 3 workers, V. P. DA SILVA [MZSP]. S ã o P a u l o : Adamantina, 15.II.1990, 1 worker, 2 soldiers M. L. DE ANDRADE [SMNS]; Agudos, 11.X.1953, 4 workers, W. W. KEMPF [MCZC]; Anhembi, Fazenda Barreiro Rico, 14.II.1962, 4 workers, W. W. KEMPF et al. [MZSP]; Anhembi, 19.III.1966, 3 workers, R. GRANTSAN [MZSP]; Araçatuba, Oct. 1961, 6 workers, J. LANE & RABELLO [MZSP]; Bauru, Rio Ferro, 27.XI.1905, 5 workers, J. LIMA [MZSP]; Caiuá, Fazenda Santa Lucília, 03.I.1971, 1 worker, C. CRUZ-LANDIM [MZSP]; Castilho, left side of Rio Paraná, 14.X.1964, 2 workers, Exp. Depto. Zool. [MZSP]; Esperança do

Sul, Fazenda Itaquerê, 20.VI.1965, 26 workers, 28.IV.1968, 2 workers, K. LENKO [MZSP]; Guararapes, January 1995, 1 worker, F. MARICATO; Inubia Paulista, 05–10.I.1973, 15 workers, P. BOVEY [MHNG]; Ipauçu, 20.IX.1928, 4 workers, B. S. PESSOA [MZSP]; Itápolis, Fev. 1960, 2 workers, B. SCHWEITZER [MZSP]; Ituverava, 1911, 4 workers, E. GARBE [MZSP]; José Bonifácio, 31.VII.1970, 3 workers, J. M. DINIZ [MZSP]; Juquiá, Nov. 1929, 2 workers, J. LANE [MZSP]; Lençóis, Jul. 1928, 4 workers, D. MENDES [MZSP]; Limeira, 09.IV.1953, 8 workers, RABELLO [MZSP]; Lins, several workers, a gynandromorph, V.1995, A. L. DE ANDRADE; same locality, 06.IX.1995, many workers, soldiers, gynes and males, M. L. DE ANDRADE [MNHN, USNM, ZSMN]; Mirassol, 16.VIII.1968, 1 worker, P. DE BIASI [MZSP]; Mirassol, (coqueiro), 15.XI.1964, 3 workers, G. BAUAB [MZSP]; Morro Pelado, Jun. 1964, 1 worker, EDWALL [MZSP]; Nova Granada, Fazenda Guariroba, Mar. 1960, 6 workers, J. LANE [MZSP]; Nova Europa, Fazenda Itaquerê, 24–31.VIII.1965, 7 workers, LENKO & PEREIRA [MZSP]; Piracicaba, ESALQ, 15.IX.1967, 1 worker [MZSP]; Piracicaba, Nov. 1906, 3 workers, J. LIMA [MZSP]; Piracicaba, 12.VI.1990, 6 workers, F. A. G. MELLO MZSP]; Porto Cabral, Rio Paraná, 01–25.IV.1944, 1 worker, TRAVASSOS FILHO, CARRERA & E. DENTE [MZSP]; Porto Epitácio, Oct. 1926, 1 worker, LIMA [MZSP]; Rio Claro, Nov. 1930, 4 workers, MARTINHO [MZSP]; Ribeirão Preto, Col. S. Amália, 12.VI.1927, 2 workers, O. CONDE [MZSP]; Ribeirão Preto, Fac. de Medicina, 09.IX.1973, 6 workers, M. T. DA SILVA [MZSP]; Rio Claro, Dec. 1942, 1 worker, P. S. PEREIRA [MZSP]; São Carlos, I. 1962, 6 workers, L. STOWBINENKO [MZSP]; São Paulo, Santo Amaro, I.1963, 1 worker, J. LANE [MZSP]; Serra Negra, 11.X.1987, 3 workers, L. C. FORTI [SMNS]; Tupã, 18.II.1990, 2 workers, M. L. DE ANDRADE [SMNS]. Paraná: Querência do Norte, 23.VII.1974, 3 workers, A. B. BARTOSAECK [MZSP]; Rolândia, Dec. 1945, Set. 1959, 13 workers, W. W. KEMPF [MZSP]; Rondon, Jul. 1952, 2 workers F. PLAUMANN [MZSP].

Peru: Cumbace (not located), 1 worker [MCSN].

Bolivia: no further locality, 2 workers [MHNG]; Río Guapo, 1 worker, LIZER [MZSP].

Argentina: Formosa: Clorinda, 2 workers [MCZC]; Formosa, 18.X.1900, 2 workers, 1 gyne [MCSN]. Salta: Urundel, 28.XI.1948, 1 worker, 1 soldier, N. KUSNEZOV [MZSP]. Misiones: Eldorado, km 47, 04.X.1967, 1 worker, A. KOVACS [MHNG]; Esperanza, 10.VIII.1973, 1 worker, A. KOVACS [MHNG]; Mado, 19.VIII.1971 and 1973, 2 workers; Leandro, N of Alem, 22.2.1958, 36 workers, 1 soldier, N. KUSNEZOV [MHNG]; Iguassú (? = Puerto Iguazú), 14–17.1.1938, 3 workers, F. TIPPMANN [ZSMC].

Paraguay: no further locality, 2 workers, 1 gyne, BOHLS [MCSN]. Amanbay: Bella Vista, 23.X.1979, 9 workers, Expéd. Muséum Genève [MHNG]. La Cordillera: San Bernardino, 7 workers, 2 soldiers, 3 gynes, 1 male, K. FIEBRIG [MHNG, ZSMC, USNM]. Guaíra: Villarica, 3 workers [MCZC]; Puerto Bertoni, 1 worker, SILVESTRI [MHNG]. Misiones: Isla Yaciretá, 08.XII.1974, 6 workers, P. DUELLI [MZSP]; Cap. Mesa, 31.X.1974, 1 worker, P. DUELLI [MZSP]. Alto Paraná: Pastoreo, 30.IX–04.X.1974, 25 workers, P. DUELLI [MZSP].

Discussion. - *C. clypeatus* shares with *membranaceus* and *ustus* several characters, the most visible of which is the gaster surrounded by a broad lamella. These three species can be easily distinguished by the colour and by the consistency of the lamellae around the body. KEMPF (1973) states that *clypeatus* is the most "advanced" species of his *clypeatus*-group (which is perfectly equivalent to our *clypeatus* clade and to the genus *Zacryptocerus* of WHEELER), although *membranaceus* (q. v.) exhibits a more specialised cephalic morphology in the soldier and in the gyne.

FERNÁNDEZ et al. (1996) report this species also from the Colombian state of Meta.

The record of this species from the Island Margarita by JAFFE & LATTKE (1994), confirmed by our own examination of material from the same provenance, is the sole record of *Cephalotes* from the French and Venezuelan Lesser Antilles.

Distribution: Colombia, Trinidad & Tobago, Venezuela, Guyanas, Brazil, Peru, Bolivia, Argentina, Paraguay.

Cephalotes membranaceus (KLUG)

Cryptocerus membranaceus KLUG, 1824: 208. Worker. Original description. Type locality: Brazil. Type material: not available for the present study.

Cryptocerus fervidus SMITH, 1876: 208, pl. 11, fig. 1. Gyne. Original description. Type locality: Rio de Janeiro. Type material: holotype gyne in BMNH (KEMPF, 1964 a: 438), examined. Synonymy by KEMPF, 1958 a: 135.

Cephalotes membranaceus (KLUG), EMERY, 1914: 39. First combination in *Cephalotes*.

Zacryptocerus membranaceus (KLUG), EMERY, 1915 a: 192. First combination in *Zacryptocerus*.

Zacryptocerus membranaceus (KLUG), KEMPF, 1951: 141, figs. 106, 110. Worker.

Zacryptocerus membranaceus (KLUG), KEMPF, 1973: 452, figs. 2, 5, 6. Worker, soldier, gyne.

D i a g n o s i s . - A member of the *clypeatus* clade characterised in the worker and in the soldier by the body light ferruginous-brown with the head, mesosoma, pedicel and gaster surrounded by a semitransparent lamellaceous border, and, in the soldier and in the gyne, by the head with an incomplete disc.

W o r k e r (description of KEMPF, 1951). - "Length 5.6 mm. Median head length 1.46 mm. Weber's length of thorax 1.58 mm. Ochraceous, darker than the preceding species [*clypeatus*], subopaque, strongly shagreened.

Head transverse. Frontal carinae not hyaline, semiopaque, due to strong sculpture; rounded anteriorly, sinuate laterally and strongly upturned, vertical and lobate above the eyes. Occipital angle dentate with a broad, blunt, stout tooth projecting from beneath. Eye stalk not completely united with frontal carinae, the apical end free.

Thorax similar to that of *clypeatus*, except the sculpture. Scapular spines more recurved. No trace of transverse pronotal crest. Mesonotal tooth slender, cylindrical, and pigmented. Mesoepinotal suture more or less distinct. Epinotal spine developed, projecting belong the enveloping border. Legs lacking foveolae. Femora angulate above, greatly inflated, upper face marginate distad, beginning from the angle. Basitarsus not quite as broad as in *clypeatus*.

Petiole transverse, slightly narrower than in *clypeatus*, lateral spines slender, blunt at apex, very little upturned. Ventral face with a small midventral hyaline tooth. Postpetiole slightly longer than petiole, the lateral teeth about half as long as the total width of the body.

Gaster circular, broadly surrounded by a horizontal, coarsely sculptured, laminate border which is notched mesially behind.

Foveolae indistinct to obsolete; pilosity consisting of long, silvery, appressed, and scale-like hair."

Measurements (in mm) and indices: TL 6.56–7.36; HL 1.52–1.74; HW 2.44–2.70; EL 0.28–0.32; PW 2.52–2.88; PeW 0.95–1.08; PpW 0.89–1.04; HBaL 0.66–0.80; HBaW 0.23–0.25; CI 155.2–161.2; PI 93.7–100.0; PPeI 265.3–275.0; PPpI 276.9–286.9; HBaI 31.2–34.8.

S o l d i e r (description of KEMPF, 1973). - "Total length 8.0 mm; head length 2.56 mm; maximum head width 2.97 mm; maximum diameter of eyes 0.34 mm; Weber's length of thorax 2.59 mm; maximum width of pronotum 3.03 mm; gaster length 3.08 mm; gaster width 2.84 mm. Differs from the respective worker in the ensuing characters: Cephalic disc with sides subparallele, scarcely converging in front except for the anterior curvature; integument only superficially punctulate, quite shining, and densely foveolate bearing a simple appressed hair; vertex with a mesially strongly bidentate, transverse carina that attains the lateral margin at both sides; occiput vertically truncate behind this carina; eye stalk not detached from the head proper, yet between the upper orbit of eye and the rim of cephalic disc is a deeply excavated groove; thorax similarly sculptured as head on dorsum and sides of pronotum, the latter with a strongly elevated, foliaceous transverse carina on dorsum which is semicircularly excised in the middle; in side-view, the anterior portion of the pronotum in front of the carina forms a right angle with the posterior portion behind the carina and the mesonotum; membranaceous borders of pronotum and propodeum narrower and the enclosed spines stronger, those of the propodeum shorter and more upturned; gaster relatively more elongate and membranaceous border laterally somewhat narrower.

Intermediates have the transverse pronotal carinae more or less developed and the thoracic dorsum foveolate, but the cephalic sculpture is unvariably as in the worker, and they also lack the bidentate carina on vertex".

Measurements (in mm) and indices: TL 8.44–9.08; HL 2.08–2.16; HW 2.88–3.00; EL 0.32–0.34; PW 3.00–3.04; PeW 1.16–1.20; PpW 1.08–1.12; HBaL 0.80–0.82; HBaW 0.27–0.28; CI 138.5–138.9; PI 94.7–100.0; PPeI 253.3–258.6; PPpI 271.4–277.8; HBaI 32.9–35.0.

Gyne (description of KEMPF, 1973). - "With the same features as the soldier, but the head is rather subquadrate than transverse; transverse carinae of vertex and pronotum much lower, the former bidentate in the middle; thorax and gaster lacking the encircling, semitransparent, laminate borders, except for the anterolateral corners of tergum I of gaster. Differs from the female of *clypeatus* as follows: integument subopaque, finely and densely punctulate throughout; foveolae on cephalic disc and thoracic dorsum denser, crowded; vertex of head with a transverse carina besides the pair of teeth; transverse carina of pronotum more elevated and foliaceous; propodeal spines longer and subacute; first tarsomere of hind leg long, not longer than, as tarsomeres 2 – 5 combined; lateral spines of postpetiole longer, about one half as long as length of postpetiole; tergum I of gaster anterolaterally narrowly crested but lacking the white spots encircled with black on each corner".

Measurements (in mm) and indices: TL 11.76–12.40; HL 2.16–2.28; HW 2.44–2.68; EL 0.40–0.44; PW 2.60–2.68; PeW 0.82–0.92; PpW 1.24–1.32; HBaL 0.88–0.94; HBaW 0.28–0.29; CI 110.9–117.5; PI 91.0–101.5; PPeI 286.9–317.1; PPpI 200.0–209.7; HBaI 30.8–32.9.

Material examined. - **Brazil**: without further locality, 2 workers [MHNG, NHMB]. Espírito Santo: Santa Teresa, 1 worker, O. CONDE [MZSP]. Rio de Janeiro: no further locality, 1 gyne (holotype of *fervidus* SMITH) [BMNH]; Corcovado, 2 workers [MHNG]; same locality, 10.XI.1958, 2 gynes, SEABRA & ALVARENGA [MZSP]; Represa Rio Grande, 15.III & IV.1961, 42 workers, 2 soldiers, F. M. OLIVEIRA [MCZC, MZSP]; Niterói, Horto, 28.XI.1932, 1 worker, AJAX [MZSP]; Rio de Janeiro, 1883, 1 worker, P. GERMAIN [MCSN].

Discussion. - We are inclined to regard *membranaceus* as the most specialised species of the *clypeatus* clade. The soldier and the gyne of this species have traces of a cephalic disc, missing in the other related species. The closest relative of *membranaceus* is *clypeatus* and both species, *clypeatus* and *membranaceus*, share the propodeal spines of the soldier strongly curved up- and forwards.

Distribution: Brazil.

5.6.8. The *multispinosus* clade

This clade is characterised by only one synapomorphy: the reduced propodeal lamella (char. 34, state 1). It comprises a Mexican and two Dominican fossils and three Recent Mesoamerican species. The outgroup of the clade is the *clypeatus* clade. It is remarkable that the first species of the *multispinosus* clade (*C. poinari*) still exhibits the general habitus of the members of the *clypeatus* clade though missing three of the four synapomorphies of it. The fourth synapomorphy of the *clypeatus* clade (CI > 155) is present also in *poinari* but it results homoplastic with the one of the *clypeatus* clade under any customary assumption on character evolution. KEMPF (1951) supposed that *biguttatus* and "*multispinosus*" (= *goniodontus*) represent a distinct subgroup of his *pavonii*-group. Our cladogram suggests a paraphyletic position for *biguttatus* and *multispinosus* as compared with the *pavonii* clade. This forces us to regard these two species plus one Recent and three fossil ones closely related to them as a separate clade sharing with the species of the *pavonii* clade and

with *umbraculatus* (the unique member of its own clade) the angle between the basal and declivous faces of the propodeum ≥ 110°.

Species included in the clade: *biguttatus*, *goniodontus*, *hispaniolicus*, *multispinosus*, *poinari*, *squamosus*.

† *Cephalotes poinari* BARONI URBANI new species
Figs. 14 D, 126

Type material: Holotype worker (unique) in Mexican amber GOPC No. Mex. 2–2.

Derivatio nominis: this species is named after Dr. George O. Poinar, Jr. who gave us this and many more superb amber specimens for study.

Diagnosis. - A member of the *multispinosus* clade differing from all the other species of the clade, in the worker, by the CI > 155.

Worker (Fig. 126). - Head broader than long. Frontal carinae not upturned above the eyes. Vertexal angles with broad, round lamella and with weakly crenulate margin. Vertexal margin concave and with a salient "neck" medially. Vertex without denticles. Eyes strongly protruding. Mandibles laterally angulate.

Mesosoma. Scapular angles absent. Anterior pronotal border straight. Pronotal sides with a strongly projecting, broad, long, anteriorly truncate, semitransparent lamella. Promesonotal suture superficially impressed. Sides of the mesonotum armed with a pair of obtuse teeth. Propodeal suture impressed. Propodeum with differentiate basal and declivous faces; sides of the basal face straight; sides of the declivous face with a broad, obtuse, semitransparent, lamellaceous triangular expansion.

Petiole with truncate anterior face. Petiolar and postpetiolar dorsum concave and bicarinate. Petiolar sides with a broad, round, semitransparent lamella medially. Postpetiolar sides anteriorly with another broad, obtuse, semitransparent lamella.

Gaster round and with a pair of broad, anterolateral lamellae.

Fore coxae angulate. Mid and hind femora angulate. Mid basitarsi flat.

Sculpture. Head minutely reticulate-punctate and with superficial foveae larger than their interspaces, diminishing in size anteriorly, rare on the frontal carinae. Ventral face of the head with the same type of sculpture as on the anterior part of the dorsum. Pronotum sculptured as the posterior part of the head dorsum but with sparser foveae. Mesonotum reticulate-punctate and with foveae larger than those on the pronotum. Basal face of the propodeum reticulate and with irregular, dense foveae. Pedicel reticulate-punctate and with rare, small foveae. Declivous face of the propodeum, pleurae, gastral tergites, sides of the first gastral sternite, remaining sternites and legs strongly reticulate. Mesopleurae with additional, thin, longitudinal rugosities. First gastral tergite longitudinally rugulose close to the articulation with the postpetiole. Centre of the first gastral sternite superficially shining.

Pilosity. Each fovea with a thin, appressed hair. Border of the vertexal angles and peduncular expansions with rare hairs of two types (1) short, slightly clubbed and (2) pointed and longer than the type (1). Posterior border of the gastral tergites and of the sternites with long, pointed hairs.

Colour. Frontal carinae, vertexal angles, pronotal lamellae, propodeal lamellae and gastral lamellae dark orange and semitransparent.

Measurements (in mm) and indices: TL 5.06; HL 1.02; HW 1.87; EL 0.18; PW 1.62; PeW 0.55; PpW 0.65; CI 183.3; PI 115.4; PPeI 294.5; PPpI 249.2.

Material examined. - **Mexican amber**: 1 worker (holotype) in the GOPC (reference number: Mex. 2–2); a possible (then aberrant), second specimen of this species (reference number Mex. 2–3) in the GOPC.

Discussion. - *C. poinari* is the outgroup of all the remaining species included in the *multispinosus* clade. It shares with *hispaniolicus* (the first ingroup

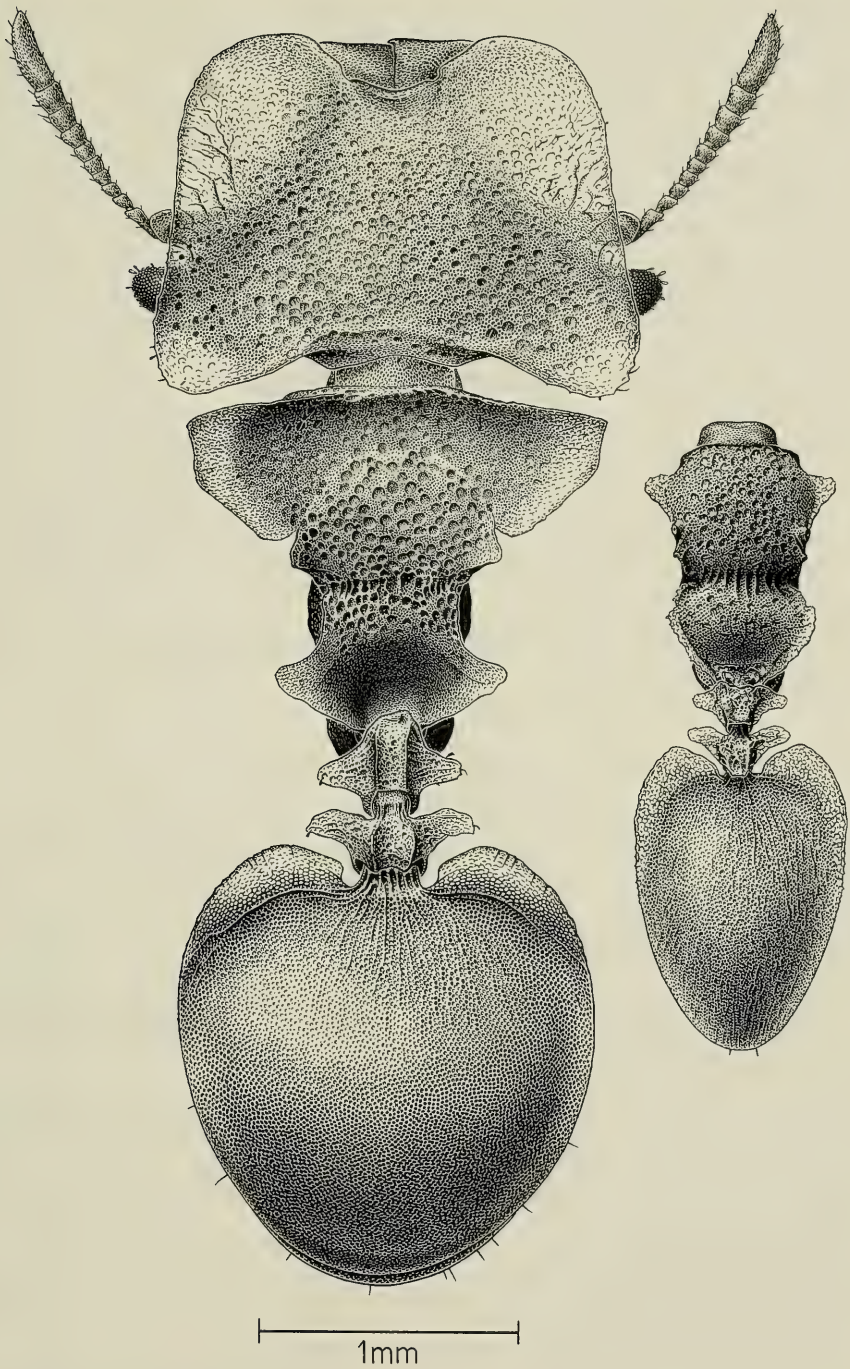


Fig. 126. *Cephalotes poinari* BARONI URBANI from Mexican amber. Worker (holotype) in dorsal view, left, and putative dwarf worker embedded in the same amber sample (right). Appendages omitted.

species) the vertex without denticles and the propodeal lamellae inserted after the beginning of the basal face. *C. poinari* differs from *hispaniolicus* by the shape of the propodeal lamellae: triangular, projecting and pointed, instead of narrow and obtuse.

The study of the amber specimen Mex. 2 in which the holotype of *C. poinari* is included proved puzzling in several respects since it contains three different *Cephalotes* specimens. One of them will be described in this paper as a second new species belonging to another clade (*grandinosus*). The third specimen (Mex. 2–3) is without head but differs markedly from the former two specimens. We think it unlikely that three different species of *Cephalotes* may have been trapped in the same 4.2 x 2.7 cm amber sample, though, among Recent species, it is not uncommon to have three species nesting in different parts of the same tree. The specimen Mex. 2–3 (Fig. 126, right), additionally, is much smaller than the holotype of *poinari*, but it bears with it a general morphological resemblance further stressed by remarkable similarities in microsculpture. For some time we caressed the idea that the specimens Mex. 2–2 and Mex. 2–3 may represent simply worker and soldier of the same species, but we had to abandon our belief since no "true" soldier characters, like pronotal carina and vertexal spines can be detected in *poinari*. We already wrote that the possibility to have three species represented by three specimens in the same amber sample appears remote to us; the sole alternative remaining is to consider the specimen Mex. 2–3 as a dwarf, aberrant *poinari* worker.

Note: The drawing, based on the holotype, shows the gaster, dorsally, in slightly inclined view since an optimal, perfectly dorsal view was not possible.

Distribution: Mexican amber.

† *Cephalotes hispaniolicus* DE ANDRADE new species

Figs. 13 D, 127

Type material: Holotype worker (unique) in Dominican amber, SMNS Do–4163.

Derivatio nominis: *hispaniolicus* is a neologism indicating the provenance from the island of Hispaniola.

Diagnosis. - A member of the *multispinosus* clade differing from its outgroup species, *poinari*, for the CI < 143 and from its ingroup species for the absence of vertexal denticles.

Worker (Fig. 127). - Head only slightly broader than long. Frontal carinae not upturned above the eyes. Vertexal margin concave and with a short "neck" medially. Vertex without denticles. Eyes not strongly protruding. Mandibles laterally angulate.

Mesosoma. Scapular angles absent or not visible in dorsal view. Pronotum protruding anteriorly; anterior pronotal border straight. Pronotal sides with a long, semitransparent lamella obliquely truncate in front. Promesonotal suture absent Sides of the mesonotum nearly unarmed. Propodeal suture impressed. Propodeum with weakly differentiate basal and declivous faces; sides of the basal face anteriorly straight, posteriorly bearing a lamellae, obtuse anteriorly and prolonging backwards to the declivous face.

Petiole without distinct anterior and posterior faces. Petiolar and postpetiolar dorsum concave and weakly bicarinate. Petiolar sides with a broad, round, semitransparent lamella medially. Postpetiolar sides anteriorly with another broad, pointed, semitransparent lamella.

Gaster suboval and with a pair of broad, anterolateral lamellae.

Fore coxae angulate. Mid and hind femora angulate. Mid and hind basitarsi flat and with broad base.

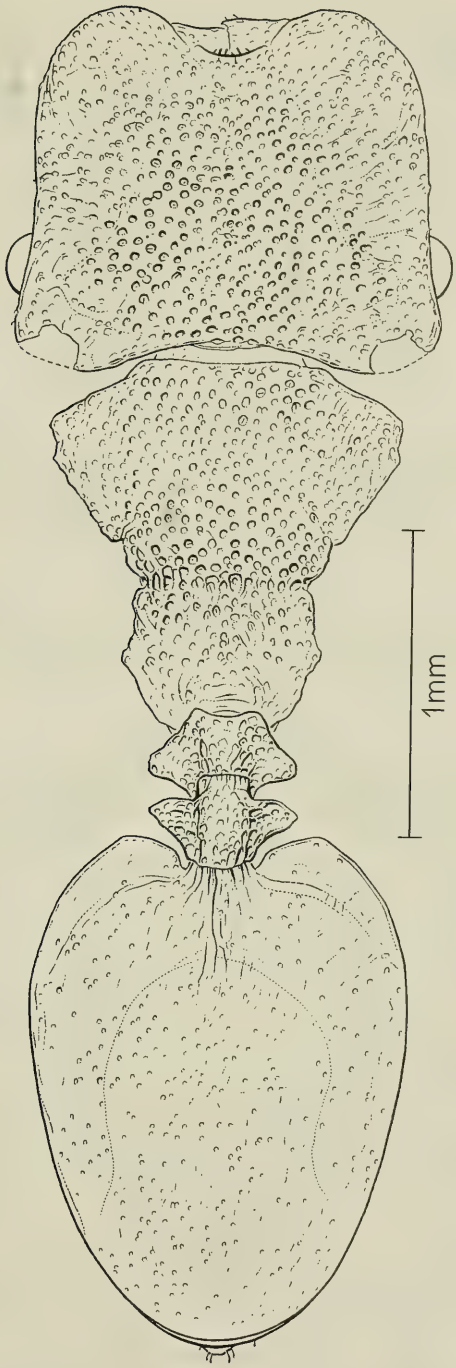


Fig. 127. *Cephalotes hispaniolicus* DE ANDRADE from Dominican amber. Worker in dorsal view. Appendages omitted.

Sculpture. Head minutely punctate and with superficial foveae variably clumped diminishing in size anteriorly. Ventral face of the head with the same type of sculpture as on the anterior part of the dorsum. Mesosoma minutely reticulate and with foveae as broad as their interspaces, the foveae less regular on the propodeum. Peduncular segments with the same type of sculpture as on the propodeum but denser. Pleurae, gaster and legs reticulate. Centre of the first gastral sternite superficially shining.

Pilosity. Each fovea with a thin, appressed hair; similar hairs on the gaster. Border of the vertexal angles with rare, minute, clubbed hairs. Posterior border of the gastral tergites and of the sternites with clubbed hairs of variable size.

Colour. Frontal carinae, pronotal lamellae, propodeal lamellae and gastral lamellae dark brown and semitransparent.

Measurements (in mm) and indices: TL 4.39; HL 0.98; HW 1.40; EL 0.20; PW 1.15; PeW 0.49; PpW 0.50; HBaL 0.47; HBaW 0.18; CI 142.8; PI 121.7; PPeI 234.7; PPpI 230.0; HBaI 38.3.

Material examined. - **Dominican amber**: 1 worker (holotype) in the SMNS (reference number: DO–4163).

Discussion. - *C. hispaniolicus* results as the second ingroup species of the clade (after *poinari*) and, in turn, outgroup of all remaining species. Its affinities, however, are much greater with the Mexican fossil *poinari* than with the next ingroup species (the equally Dominican fossil *squamosus*). *Hispaniolicus* shares with *poinari* broad (as compared with those of the other ingroup species) lamellar expansions of the mesosoma, one of the two highest CI's within the clade, and a superficial sculpturation.

Distribution: Dominican amber.

† *Cephalotes squamosus* (VIERBERGEN & SCHEVEN) new combination
Figs. 7 C – 10, 11 D, 17 C & D, 128, 129

Zacryptocerus sp., SCHLEE, 1980: 39, pl. 22. Worker.

Zacryptocerus sp., BARONI URBANI & SAUNDERS, 1980: 222, pl. 2 fig. 1. Worker.

Paracryptocerus sp., POINAR, 1992: 208, figs. 106, 107. Worker.

Zacryptocerus squamosus VIERBERGEN & SCHEVEN, 1995: 163, figs. 6 a-d. Worker. Dominican amber. Original description. Type material: holotype and two paratypes in the collection JSHC, examined, one paratype MCZC–5, examined.

Zacryptocerus pseudo-aztecus (sic) VIERBERGEN & SCHEVEN, 1995: 163, figs. 7 a-d. Worker. Dominican amber. Original description. Type material: holotype in JSHC, one paratype worker in MCZC–3, examined. New synonym.

Diagnosis. - A member of the *multispinosus* clade characterised, in the worker, by the vertex with a pair of denticles, as compared with its outgroup species, and by the long pronotal lamellae and absence of gastral spots as compared with the ingroup species.

Worker (Figs. 128, 129). - Head subquadrate. Frontal carinae superficially crenulate and gently upturned above the eyes. Vertexal angles round and with weakly crenulate margin. Vertexal margin concave medially. Vertex with a pair of denticles. Mandibles laterally angulate.

Mesosoma. Scapular angles absent. Anterior pronotal border straight, protruding anteriorly and passing into the sides with a long, weak concavity. Pronotal sides with a broad, long, continuos lamella with semitransparent border; anterior half of the lamella truncate in some specimens. Promesonotal suture often superficially impressed. Sides of the mesonotum unarmed or with a pair of round or truncate teeth. Propodeum with differentiate basal and declivous faces; sides of the basal face marked anteriorly and posteriorly by an angle;

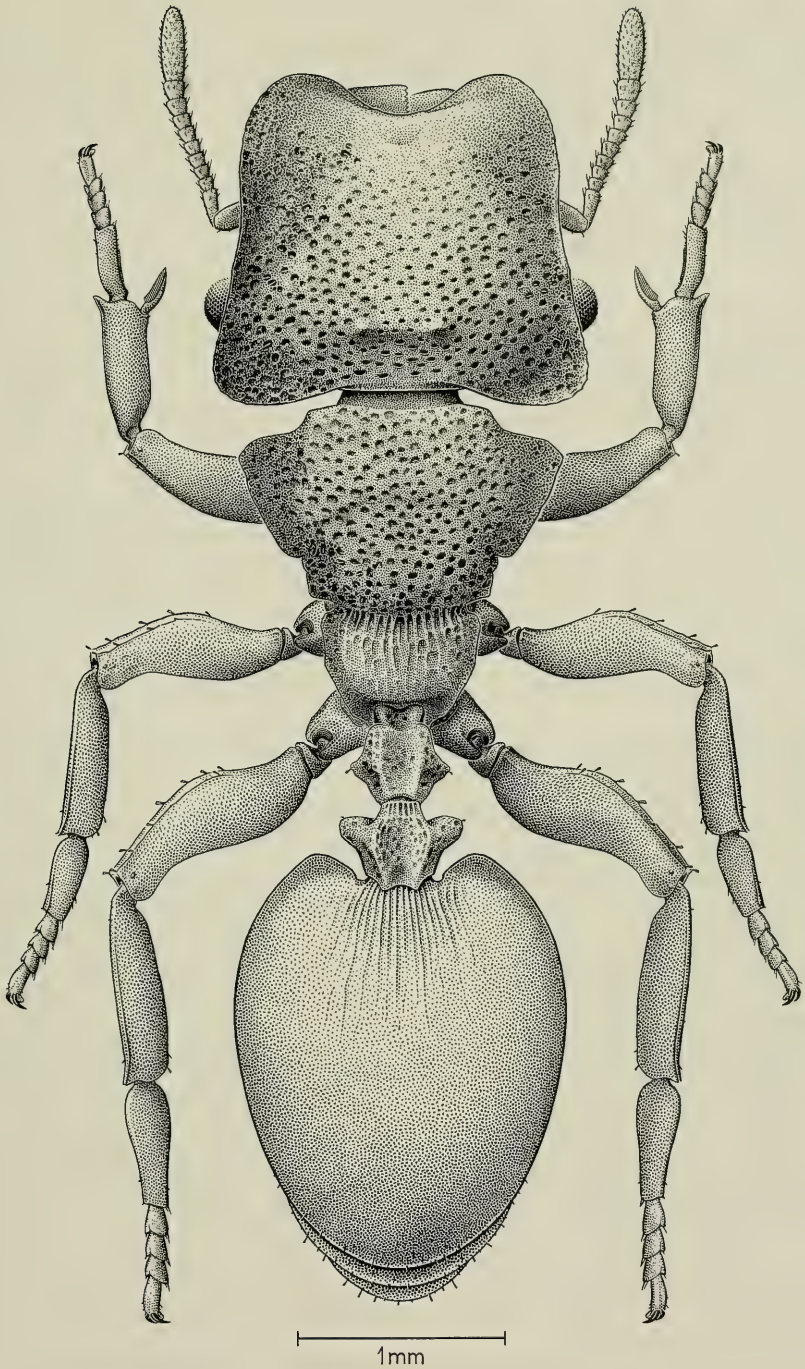


Fig. 128. *Cephalotes squamosus* (VIERBERGEN & SCHEVEN) from Dominican amber. Worker in dorsal view.

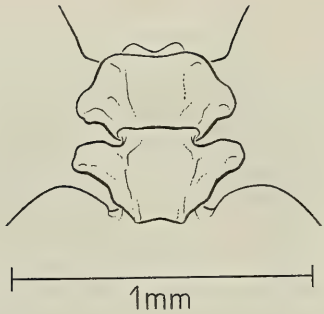


Fig. 129. *Cephalotes squamosus* (VIERBERGEN & SCHEVEN) from Dominican amber. Petiole and postpetiole of the worker exemplifying another possible morphology Transitional forms between the morphology illustrated here and that of Fig. 128 are frequent.

declivous face of the propodeum converging posteriorly; some specimens with a semitransparent lamella beginning at some distance after the basal face and narrowing backwards.

Petiole. Anterior face short and obliquely truncate, posterior face gently sloping anteriorly and concave medially. Petiolar sides with a pair of obtuse or round teeth medially. Postpetiolar node concave in the middle; anterior half of the postpetiolar sides with a pair of broad, round teeth.

Gaster suboval, with a pair of anterolateral, variably developed, lamellae.

Fore coxae angulate. Mid and hind femora angulate. Mid and hind basitarsi flat and with broad base.

Sculpture. Head minutely reticulate-punctate and with foveae about of the size of their interspaces, diminishing in size anteriorly, rare on the anterior fourth. Ventral face of the head with the same type of sculpture as the dorsum of the head and superimposed to irregular, anastomosing rugosities. Pronotum and mesonotum minutely reticulate-punctate and with foveae as broad as their interspaces; in some specimens the foveae are denser and superimposed by irregular, thin rugosities. Propodeum and pleurae reticulate and with longitudinal rugosities, the reticulation larger on the pleurae; propodeum also covered with superficial foveae variably clumped. Pedicel reticulate-punctate and with small, sparse to dense foveae. Gastral tergites, sides of the first gastral sternite, remaining sternites and legs strongly reticulate. First gastral tergite with longitudinal rugosities close to the postpetiolar insertion. Centre of the first gastral sternite shining.

Pilosity. Each fovea with a thin, appressed hair; similar hairs on the first tergite and sternite. Border of the vertexal angles, peduncular spines, legs and border of the gastral tergites and sternites with minute clubbed hairs. Posterior border of the first and second gastral sternites with rare, thin, erect, pointed hairs.

Colour. Frontal carinae, vertexal angles, pronotal lamellae, propodeal lamellae (when present) and anterolateral lamellae of the gaster ferrugineous and semitransparent. The majority of the specimens are often burned or covered by a gaseous layer preventing appreciation of the semi-transparency of the parts mentioned above.

Measurements (in mm) and indices: TL 3.96–6.52; HL 0.92–1.44; HW 1.16–1.92; EL 0.24–0.32; PW 1.00–1.68; PeW 0.43–0.56; PpW 0.46–0.68; HBaL 0.33–0.52; HBaW 0.14–0.24; CI 114.0–139.1; PI 105.1–120.7; PPeI 229.6–323.1; PPpI 210.2–262.5; HBaI 42.4–46.1.

Material examined. - **Dominican amber**: 27 workers from the SMNS (reference numbers: Do–181, Do–277-K, Do–506, Do–1978, Do–2001, Do–2043, Do–2455, Do–2700, Do–2759, Do–2807, Do–3128, Do–3316, Do–3581, Do- 3765, Do–3817, Do–3826, Do–3936, Do–3978, Do–4164, Do–4165, Do–4230, Do–4637, Do–4640, Do–4935, Do–5075, Do–5317, Do–5544); 11 workers from the GOPC (reference numbers: H 10–116–1 & 3, H 10–116–2, H 10–116 A, H 10–116 C, H 10–116 F, H 10–116 G, H 10–116 H, H 10–116 J,

H 10–117, H 10–120); 4 workers from the JSHC (holotype and 2 paratypes of *squamosus*, - holotype of *pseudoaztecus*); 13 workers from MCZC (reference numbers MCZC–5, paratype of *squamosus*, MCZC–3, paratype of *pseudoaztecus*, MCZC–1, MCZC–6, MCZC–7, MCZC–12, MCZC–14, MCZC–18 [from the amber mine La Toca], MCZC–19 [from the amber mine La Toca], MCZC–20 [from the Santiago province], MCZC–21, MCZC–22, MCZC–23); 1 worker from the NHMB (reference number PE 110).

Discussion. - Some specimens of *C. squamosus* share with *biguttatus* and with the fossil *hispaniolicus* the propodeal lamellae beginning at some distance after the basal face (char. 34, state 1), and share with *biguttatus* only a pair of vertexal denticles.

We consider all 56 specimens listed above as belonging to a single species, *squamosus*. We explain the variation observed in characters like the distance between the foveae, presence or absence of longitudinal rugosities on the mesosoma, size of the petiolar and postpetiolar expansions and head width by (geological) age differences among the specimens. The specimens GOPC H 10–116–1 and GOPC H 10–116–2 differ in turn from the others by having the sides of the pronotal lamellae truncate, the petiole and postpetiole narrower, and the anterior face of the petiole higher. If our explanation of the variability of this species is correct, however, it contradicts a recent narrowing of the age of Dominican amber by ITURRALDE-VINENT & MACPHEE (1966). Since one of the main arguments of these authors is the similarity between the fossil and the Recent fauna, the case of *C. squamosus* may represent a good counter-argument, among other possible ones. Large specimens of the Recent, phylogenetically related, *biguttatus* also have the anterior face of the petiole higher than in the smaller workers.

The holotype of *pseudoaztecus* differs from most specimens examined, except the Do–3936, by its small size, a character that we do not consider of specific value. Even less significant appear to be, in our experience, the other differential characters listed in the original description. The identity between *pseudoaztecus* and *squamosus*, already suspected by VIERBERGEN & SCHEVEN (1995), is confirmed by our study of the above material. The close relationship between *squamosus* (discussed as *pseudoaztecus*) and *bimaculatus* (discussed as *aztecus*) claimed by VIERBERGEN & SCHEVEN (1995), does not result from our character analysis. To the five characters given by these authors to separate the two species, we can add other important ones among which, for *bimaculatus*, absence of angulate femora, antennal club 2-jointed, absence of vertexal denticles, etc. Forcing *bimaculatus* and *squamosus* to be sister species would need a minimum of 9 additional steps as compared with our phylogeny (hypothesis tested by only one heuristic search with addition of taxa simple and branch swapping by TBR).

Two of the specimens examined by us have been collected in the mine La Toca supposed to host the oldest known Dominican amber. POINAR (1992) gives an age range of 30–45 Ma for the material from this mine.

Distribution. - Dominican amber.

Cephalotes biguttatus (EMERY) new combination and new status
Figs. 130, 131

Cryptocerus gibbosus biguttatus EMERY, 1890: 73, pl. 9 fig. 3. Worker, soldier and gyne. Original description. Type locality: Jiménez (Costa Rica). Type material: 7 workers, 3 soldiers, 1 gyne (syntypes) from Jiménez (Costa Rica) in MCSN, examined, 1 possible syntype

soldier without locality label in NHMB, examined, 2 syntype workers and soldiers labelled Costa Rica in MHNG, examined.

Cryptocerus gibbosus SMITH, MANN, 1922: 33. Nec SMITH, 1876. Misidentification proposed by KEMPF, 1951: 226.

Paracryptocerus multispinosus biguttatus (EMERY), KEMPF, 1951: 226, fig. 138, 152. Worker, soldier and gyne. First combination in *Paracryptocerus*.

Zacryptocerus multispinosus biguttatus, KUGLER, 1978: 474, figs. 200, 201. First combination in *Zacryptocerus*.

Zacryptocerus multispinosus biguttatus (EMERY), VIERBERGEN & SCHEVEN (1995): 168, fig. 13. Worker.

D i a g n o s i s . - A member of the *multispinosus* clade differing from its outgroup species by the presence of gastral spots and from the two ingroups by the superficial sculpture of the worker and soldier, and, in the soldier only, by the absence of cephalic disc.

W o r k e r (Fig. 130) (description of KEMPF, 1951). - "Differs from the typical form [= *multispinosus*] by the more sparsely foveolate upper surface of head, and thorax. The sides of head are somewhat converging anteriorly, not quite parallel. Mesoepinotal suture distinct. Epinotum bordered in its entire length by a continuous, converging caudad, semitransparent crest, the lower portion of the declivous face slightly impressed mesad. Laterotergite of pronotum finely reticulate-punctate, without longitudinal striae. Scales within the foveolae on head thorax and gaster more slender, longer, and silvery."

Measurements (in mm) and indices: TL 5.52–6.52; HL 1.20–1.48; HW 1.52–1.68; EL 0.32–0.39; PW 1.40–1.76; PeW 0.76–0.88; PpW 0.83–1.00; HBaL 0.54–0.60; HBaW 0.17–0.18; CI 126.7–129.0; PI 106.8–111.1; PPeI 180.0–200.0; PPpI 156.5–176.0; HBaI 30.0–31.5.

S o l d i e r (Fig. 131) (description of KEMPF, 1951). - "The soldier may be recognized by the finer sculpture on head and thorax, the foveolae are as sparse as in the worker. The teeth on the vertex have no lateral crest between the sides of the head. The occipital angles are slightly upturned in very large soldiers. Sides of mesonotum without a conspicuous, projecting, rounded lobe. Epinotum as in the worker."

Measurements (in mm) and indices: TL 7.00–7.04; HL 1.60; HW 2.04–2.06; EL 0.40; PW 1.92; PeW 0.90–0.92; PpW 1.00–1.04; HBaL 0.60; HBaW 0.19–0.20; CI 127.5–128.7; PI 106.2–107.3; PPeI 208.7–213.3; PPpI 184.6–192.0; HBaI 31.7–33.3.

G y n e (description of KEMPF, 1951). - "Length 11 mm. General color as in soldier and worker. Head longer, about as long as wide, the sides somewhat converging anteriorly. Vertex with two blunt teeth, connected by a blunt transverse crest. Occipital angles crested, subrectangular. Occiput truncate mesad and slightly excavated. Upper surface of head rather smooth, sparsely covered with small foveolae, containing a simple, appressed hair. Anterior corner of thorax rectangular, slightly notched behind the corner. Pronotum and mesonotum subfulgid, sparsely foveolate. Epinotum sharply marginate laterad, the basal face subopaque and densely foveolate, the declivous face subopaque, somewhat excavated, not foveolate. Upper mesopleura bulging, densely foveolate, the intervals rather fulgid. Lower mesopleura with a blunt tooth. Posterior portion of the sides of the thorax finely shagreened and subopaque. Femora not angulate above. Sides of petiole slightly diverging caudad until the last third, where it is suddenly constricted, forming a small tooth. Postpetiole with a short, slightly recurved, stout lateral tooth. Both peduncular segments densely but rather shallowly foveolate above. Gaster not crested antero-laterad, emarginate antero-mesad, with a large yellow spot on each anterior corner. Integument finely shagreened. Appressed hair minute. Wings infumated, veins brunneous. Fore wing with a close appendiculate marginal cell, the transverse cubital vein short to obsolete, the transverse median vein bisects the median vein into two subequal halves, the 2nd abscissa more than three times as long as the transverse median vein."

Measurements (in mm) and indices: TL 10.80–10.86; HL 1.92–1.96; HW 2.20–2.32; EL 0.44–0.48; PW 2.20–2.50; PeW 0.92–1.10; PpW 1.24–1.30; HBaL 0.72–0.77; HBaW 0.22–0.26; CI 112.2–122.9; PI 88.0–105.3; PPeI 227.3–239.1; PPpI 177.4–192.3; HBaI 30.5–33.8.

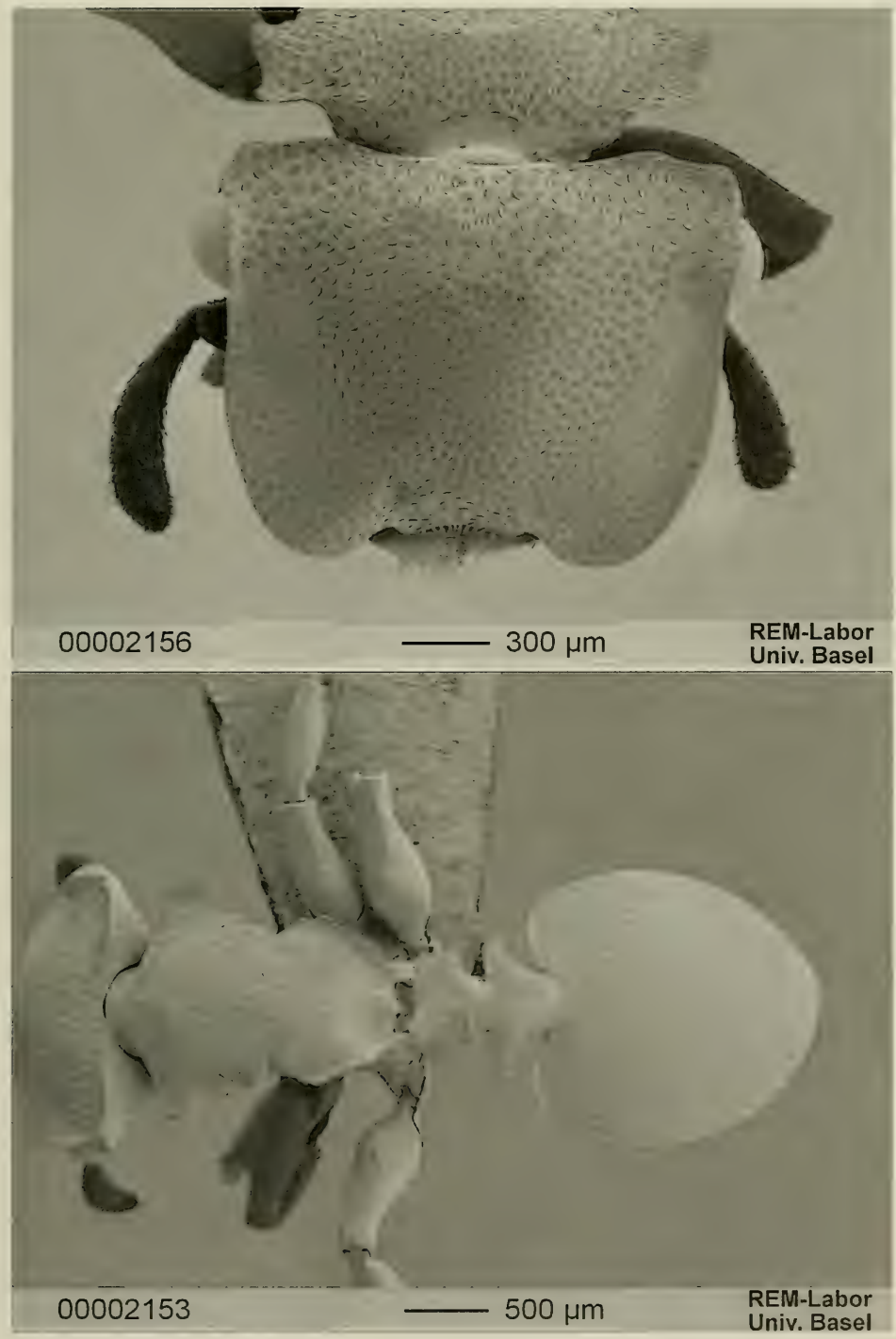


Fig. 130. *Cephalotes biguttatus* (EMERY). Worker from Turrialba (Cartago), Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

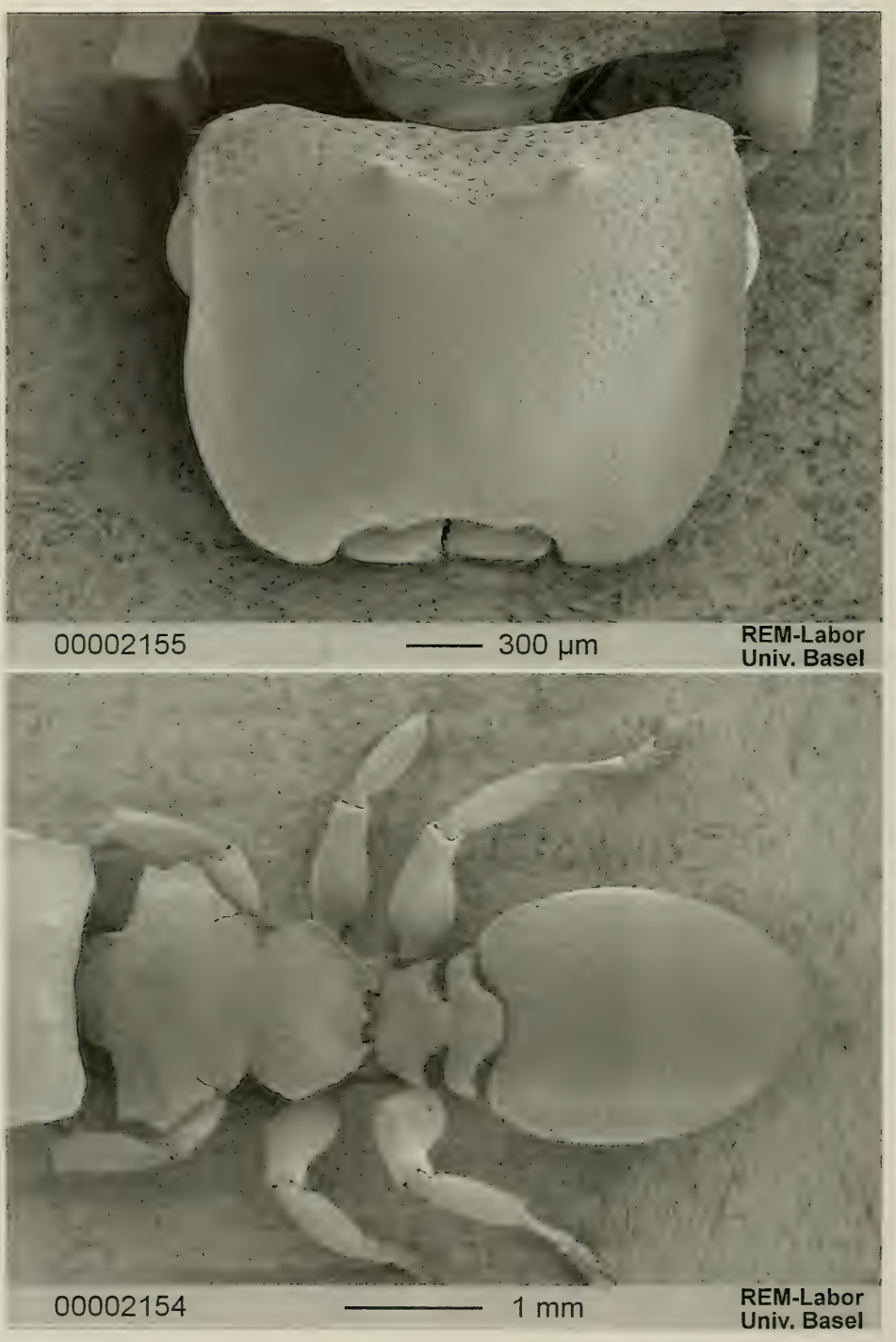


Fig. 131. *Cephalotes biguttatus* (EMERY). Small soldier from Costa Rica (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Material examined. - **Mexico**: no further locality, 1 gyne (without gaster) [MNHN].

Guatemala: Alta Verapaz, 5 mi W La Tinta, 06.VI.1974, 3 workers, P. PERKINS [USNM]; Vera Paz, Cubilguitz, Chacoj, Río Maria Linda, 3 workers, 4 soldiers, CHAMPION [MCZC, MHNG, NHMB].

Belize: San Antonio, 17.VIII.1984, on *Teobroma cacao*, 1 worker, R. A. DUNN [USNM].

Honduras: La Ceiba, 3 workers, W. M. MANN [MCZC]; La Lima, 1964, 3 workers, in *Enterolobium cyclocarpum*, C. EVERS [MZSP].

Costa Rica: without further locality, 1 soldier (? syntype) [NHMB]; 2 workers, 2 soldiers, syntypes [MCSG]; Jiménez 10 workers, 3 soldiers, 1 gyne (syntypes) [MCSN, MHNG]; Escobal, SW of Atenas, Prov. of Alajuela, 15.IX.1936, 411 m, 1 worker, A. ALFARO [MZSP]; Alajuela, 1 worker, ALFARO [MCSN]; Guápiles, 3 workers, 7 soldiers, 1 gyne, F. NEVERMANN [MCZC, MZSP]; Porto Limón, 29.IX.1908, 1 worker [MCZC]; Finca La Selva, 29.III.1979, 2 workers, T. RAY [MCZC]; Hamburg Farm, 2 workers, 2 soldiers, 1 gyne, NEVERMANN [MZSP]; Hamburg Farm, Santa Clara, VII.1924, 2 workers, F. NEVERMANN [MZSP]; Tempisque, 22.I.1937, 3 workers, A. ALFARO [MZSP]; Cartago, Prov. Turrialba, 15.VII.1965, 3 workers, F. COYLE [MZSP].

Discussion. - *C. biguttatus* appears to be the outgroup of *multispinosus* and *goniodontus* with which it shares the short pronotal lamellae. It shares with these two species and with the fossil *squamosus* the presence of spines on the vertex. Fig. 131 shows a small size soldier with pronotal carina but without cephalic disc. Large size soldiers have an incomplete disc represented by a round flattening of the posterior part of the head. The description of the soldier by KEMPF (1951) is also likely to be based on a small size soldier since large specimens examined by us show a trace of disc. The soldiers of the three species *biguttatus*, *goniodontus* and *multispinosus* appear to represent an interesting intermediate step in the evolution of the cephalic disc by having this structure incomplete. It would be of greatest interest to discover the cephalic morphology of the three fossil species belonging to the same clade and the soldier of which is still unknown.

Geographically *biguttatus* appeared to show an allopatric trend as compared with that of *multispinosus* (previously known only from S. Mexico). This distributional pattern alone would support its subspecific rank as generally regarded until today. Considering *biguttatus* as a subspecies of *multispinosus*, however, results impossible from its cladistic position at the root of both valid species *multispinosus* and *goniodontus*. *Biguttatus* and *multispinosus*, in addition, appear consistently different in microsculpture and shape of the propodeum (see e. g. Figs. 130, 134) among all the material we have been able to examine. In addition to the cladistic argument, in this paper we add also a geographic argument to consider *biguttatus* as a good species: we have a record of *multispinosus* from Costa Rica where it is likely to be sympatric with *biguttatus*.

Distribution: Mexico, Belize, Costa Rica, Honduras, Guatemala.

Cephalotes goniodontus DE ANDRADE new species
Figs. 132, 133

Paracryptocerus multispinosus (NORTON), KEMPF, 1951: 224, figs. 143, 150. Nec NORTON, 1868. Misidentification.

Type material: holotype worker from Compostela (Mexico), 22.IV.1933, W. M. WHEELER (MCZC); paratypes: 1 worker (same data as the holotype), 1 worker and 2 soldiers from vic. Compostela (Mexico), 28.V.1933, W. M. WHEELER, in MCZC.

D e r i v a t i o n o m i n i s : from the Greek γωνία (= angle) and ὀδούς (= tooth), referred to the shape of the propodeal angles.

D i a g n o s i s . - A member of the *multispinosus* clade characterised, in the worker, by the sides of the propodeum armed with a broad, triangular tooth.

W o r k e r (Fig. 132) (description of KEMPF, 1951 sub *multispinosus*). - "Length 6 mm. Median head length 1.41 mm; Weber's length of thorax 1.63. Black; the following ferruginous: Frontal carinae, tip of last funicular segment, tips of femora and tibiae. Pale yellowish: crests of thorax and peduncular spine. Yellow: a single spot on each anterior corner of the gaster.

Head subquadrate, subopaque. The anterior corners greatly rounded, the posterior corners subangulate, the sides parallel. Occipital border shallowly emarginate mesad, almost straight, with a very narrow light crest on each side. Frontal carinae not crenulate, without projecting setae from the border. Eyes very small, the maximum diameter less than 1/4 of the median head length. Vertex with a pair of small denticules. Upper surface of head densely foveolate, each foveola containing a short, broad, appressed, silvery, flat hair.

Thorax subopaque. Anterior border rounded, shoulders not separate from the lateral projections of pronotum. Sides of pronotum crested; the anterior half of the crest greatly projecting and bidenticulate, the posterior half constricted and narrow. Promesonotal suture vestigial. Mesonotum with a small lateral denticule. Mesoepinotal suture more or less distinct. Epinotum not differentiated into distinct basal and declivous faces, with a broad, large, flattened triangular tooth projecting from the anterior half of the lateral border, the posterior half carinate. Upper surface of thorax, except a small area mesially in front of the petiolar insertion, very finely shagreened, densely and coarsely foveolate, as the upper surface of head. Laterotergite of pronotum and sides of thorax finely reticulate-punctate, the laterotergite longitudinally striated, the remaining parts rugulose. Outer face of fore coxae finely longitudinally striated. Hind femora sharply angulate and denticulate above the half.

Petiole and postpetiole flattened above, the sides with a distinctly set off spine, the petiolar spine recurved, the postpetiolar spine pointing forward at base, recurved backward at apex.

Gaster subopaque, emarginate in front mesally, narrowly crested antero-laterad. All scales golden."

Measurements (in mm) and indices: TL 5.40–5.92; HL 1.24–1.36; HW 1.64–1.70; EL 0.32–0.33; PW 1.42–1.52; PeW 0.69–0.76; PpW 0.77–0.82; HBaL 0.61–0.62; HBaW 0.15–0.16; CI 125.0–132.2; PI 111.8–115.5; PPeI 205.8–211.1; PPpI 184.4–185.4; HBaI 24.6–25.8.

S o l d i e r (Fig. 133) (description of KEMPF, 1951 sub *multispinosus*). - "Length 7.7 mm. Median head length 1.78 mm. Weber's length of thorax 2.07 mm. Color as in worker. Quite similar to the worker, with the following differences: Upper surface of head subfulgid, not as shiny as in the race *biguttatus*, rather coarsely and densely foveolate. Each of the teeth on vertex sends out an oblique carina towards the sides, fading out shortly before reaching the lateral border of the head. Occipital angle rounded and crested. Pronotum with a bidenticulate lateral expansion, the sides converging obliquely towards the mesonotum behind the second denticule. Mesonotum with a blunt lateral lobe. Sculpture of thorax as coarse as on upper surface of head. Epinotum with a flat, triangular, large tooth, without a transparent crest behind. The basal and declivous faces slightly differentiated. Declivous face not excavated below. Spines of the peduncular segments shorter, less acute than in worker."

Measurements (in mm) and indices: TL (approximate from two different specimens, one without gaster and one without head) 7.10–7.28; HL 1.60; HW 2.12; EL 0.40; PW 1.88–1.96; PeW 0.85–0.89; PpW 0.90–0.98; HBaL 0.70–0.72; HBaW 0.18; CI 132.5; PI 112.8; PPeI 220.2–221.2; PPpI 200.0–208.9; HBaI 25.0–25.7.

M a t e r i a l e x a m i n e d . - **Mexico**: N a y a r i t : Compostela, 22.IV.1933, 2 workers (holotype and paratype), W. M. WHEELER [MCZC]; vic. Compostela, 28.V.1933, 1 worker (paratype), 2 soldiers (paratypes), one soldier without head and the other without gaster, W. M. MANN [MCZC].

D i s c u s s i o n . - To this species, easily distinguishable from *multispinosus* by its sculpturation and by the absence of lamellae behind the propodeal teeth, must be

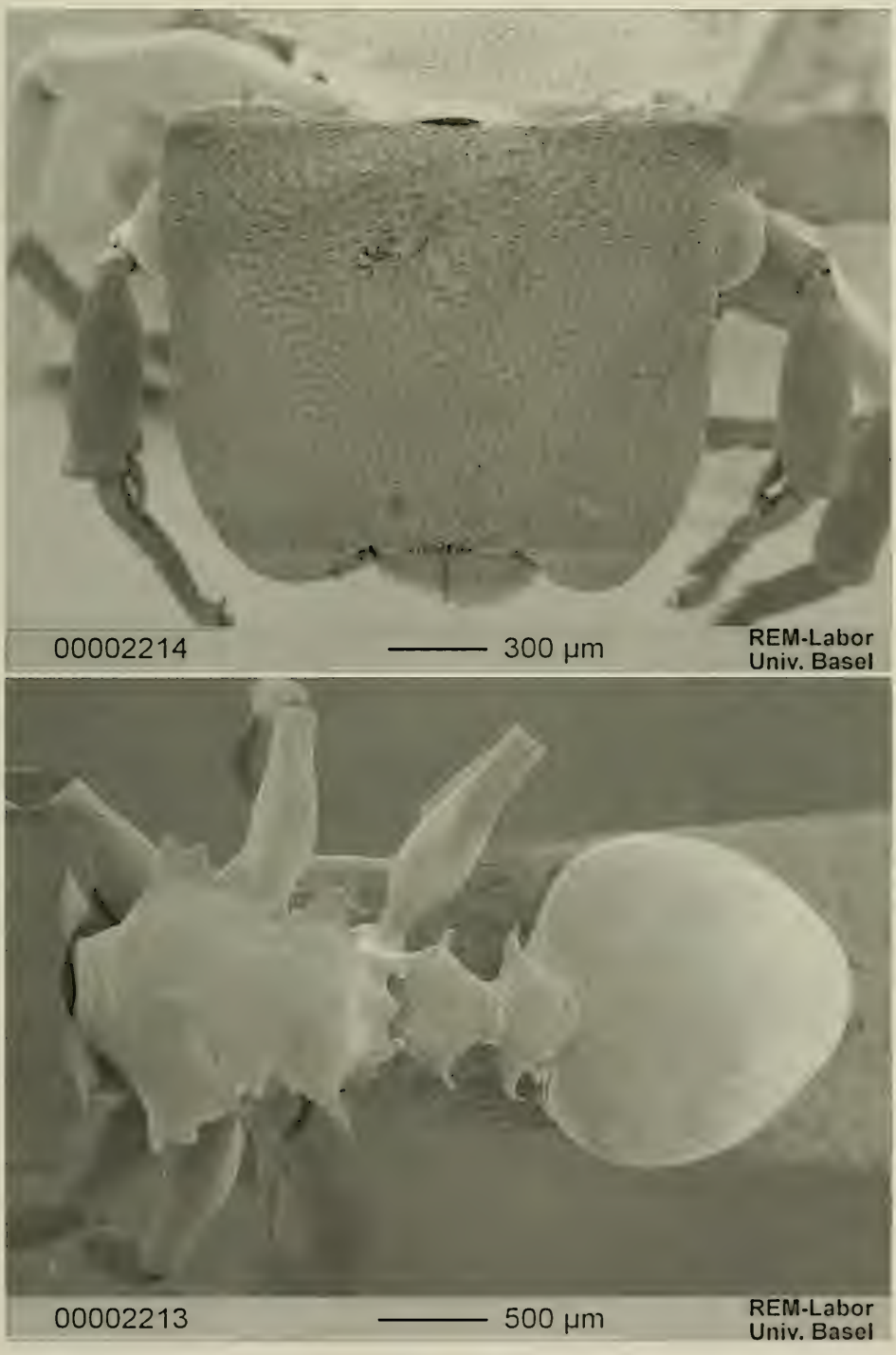


Fig. 132. *Cephalotes goniodontus* DE ANDRADE. Worker from Compostela (Nayarit), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

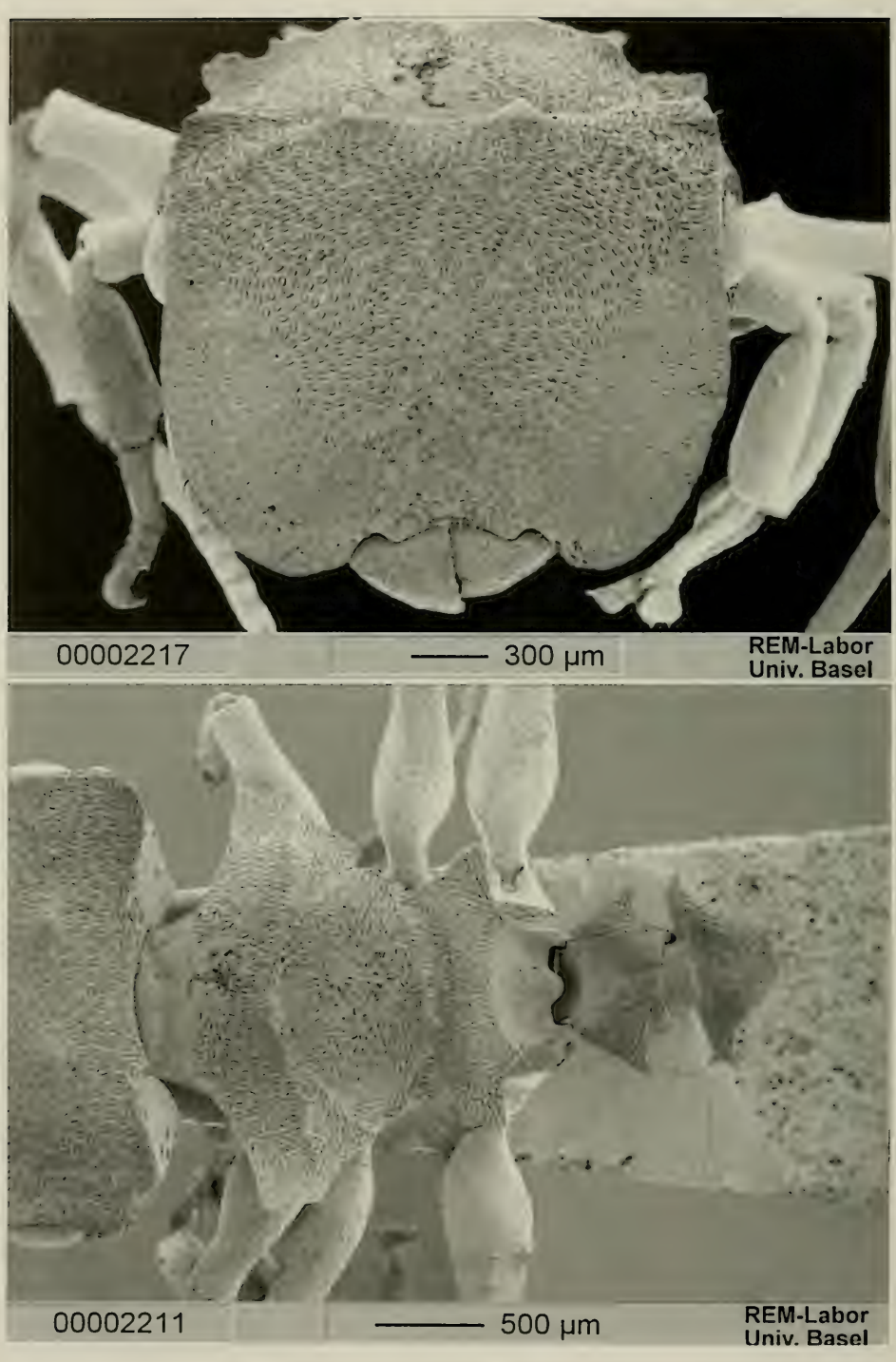


Fig. 133. *Cephalotes goniodontus* DE ANDRADE. Soldier from Compostela (Nayarit), Mexico: head (top) and mesosoma (bottom) in dorsal view.

attributed all the specimens examined by KEMPF while describing what he thought to be the true *multispinosus*.

Distribution: Mexico.

Cephalotes multispinosus (NORTON) new combination
Figs. 134, 135, 136

Cryptocerus multispinosus NORTON, 1868: 72. Worker and soldier. Original description. Type locality: Córdoba (Mexico). Type material: original specimens presumably lost. Non *Paracryptocerus multispinosus* (NORTON), KEMPF, 1951 (misidentification).

Cryptocerus gibbosus SMITH, 1876: 605, pl. 2, fig. 3. Soldier. Original description. Type locality: Mexico. Type material: holotype soldier labelled "Mexico" in BMNH, examined. Synonymy by EMERY, 1891: 167.

Cryptocerus multispinosus biguttatus EMERY, FOREL, 1899: 50. Nec EMERY, 1890. Misidentification.

Zacryptocerus multispinosus (NORTON), HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *multispinosus* clade differing from its sister species, *goniodontus*, in the worker and soldier, for the much longer propodeal lamellae, reaching the end of the propodeum posteriorly.

Worker (Fig. 134). - Head subquadrate. Eyes convex. Vertexal angles obtuse, partially lamellaceous. Vertex concave posteriorly, with a pair of denticles on the middle. Sides of the head completely marginate below. Frontal carinae broad, strongly upturned over the eyes. Clypeal border incised medially. Mandibles with a lateral tooth.

Mesosoma convex in side view. Scapular angles absent. Humeral angles with a pair of rectangular, almost transparent lamellae; the lamellae directed laterally, their sides bidentate, the posterior border narrowing posteriorly (one specimen with a round tooth instead of the posteriorly converging part). Promesonotal suture superficially impressed. Mesonotal teeth small and pointed. Propodeal suture impressed. Propodeum sloping backwards and concave posteriorly, with slightly differentiated basal and declivous faces; propodeal sides with a pair of triangular, broad, lamellaceous teeth anteriorly, narrowing medially and a broadening posteriorly. Petiole slightly narrower than postpetiole, its anterior border with a median concavity, its dorsum sloping anteriorly. Petiolar spines curved backwards, pointed, their sides not continuous with the anterior border of the petiole. Postpetiolar node slightly convex and with a superficial concavity in the middle; postpetiolar spines curved, pointed, with the apices directed backwards.

Gaster with a lamellaceous anterior border reaching the first gastral stigma.

Hind femora with a pair of small denticles in the middle; mid and hind basitarsi laterally compressed, with the basal part slightly broader than the distal one.

Sculpture. Head dorsum and mesosoma covered by integumental reticulation intermediate between the one of *biguttatus* and the one of *goniodontus*; the reticulation superimposed by foveae smaller and shallower on the anterior half of the head and on the abdominal pedicel, the reticulation more impressed on the mesosoma. Frontal carinae superficially reticulate, with small, sparse, faint foveae. Ventral face of the head slightly stronger reticulate, with sparse, faint foveae. Posterior half of the propodeum reticulate. Sides of the mesosoma reticulate, with rare to sparse foveae on the propleurae and dense, oval foveae on the posterior half of the mesopleurae and on the centre of the metapleurae. First gastral tergite reticulate and superimposed by superficial, small foveae. Corresponding sternite reticulate and slightly shining in the middle. Legs simply reticulate; distal half of femora and extensor face of tibiae covered with dense, oval foveae, this same sculpture but superficial and sparse on the remaining femora and tibiae.

Pilosity. Each fovea bearing an appressed canaliculate hair. Mandibles, vertexal angles, sides of the mesosoma, apex of the gaster and legs with slightly clavate hairs, the hairs longer on the legs and on the apex of the gaster. Sternites with rare, long, truncate hairs.

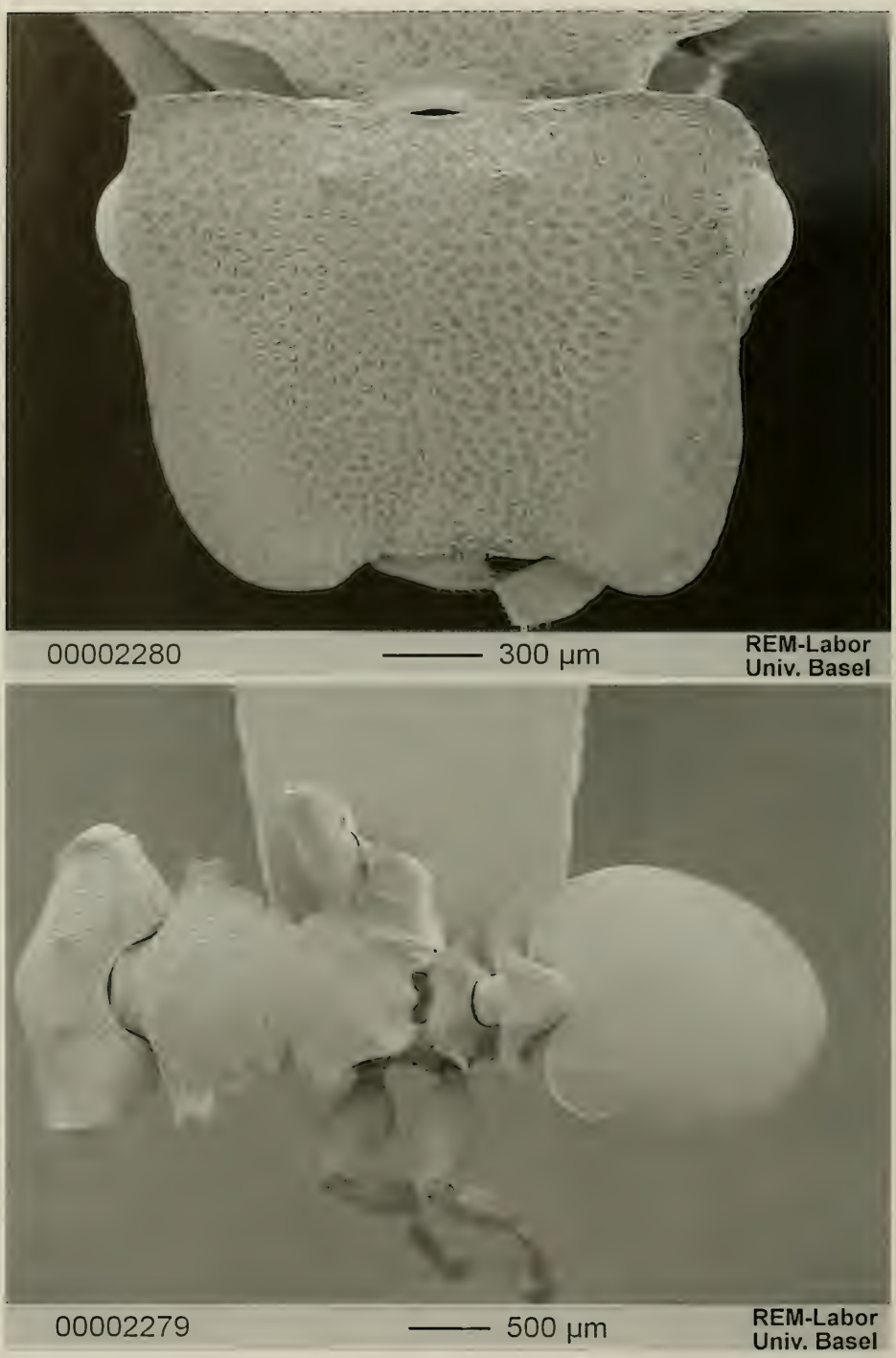


Fig. 134. *Cephalotes multispinosus* (NORTON). Worker from Mexico (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

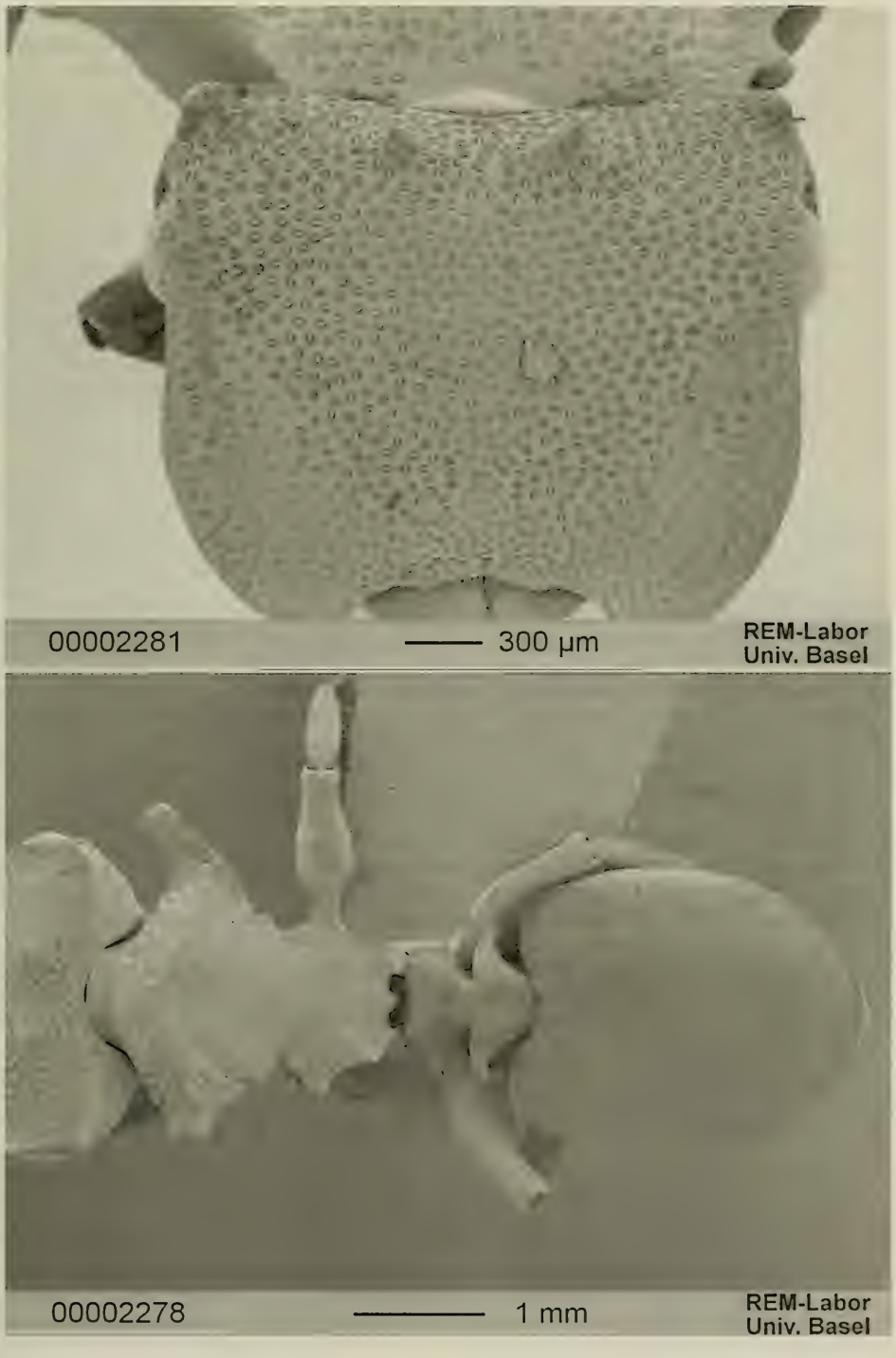


Fig. 135. *Cephalotes multispinosus* (NORTON). Soldier from Mexico (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Colour. Black. Frontal carinae, lamellae of the vertexal angles, lamellae of the mesosoma, petiolar and postpetiolar spines and lamellae of the gaster yellow to orange. Extensor face of the tibiae and tarsomeres ferrugineous. Gaster with a yellow pair of anterolateral spots.

Measurements (in mm) and indices: TL 5.10–6.00; HL 1.16–1.36; HW 1.48–1.68; EL 0.30–0.36; PW 1.24–1.52; PeW 0.71–0.77; PpW 0.80–0.88; HBaL 0.51–0.64; HBaW 0.15–0.16; CI 123.5–127.6; PI 110.5–119.3; PPeI 174.6–200.0; PPpI 155.0–172.7; HBaI 25.0–29.4.

S o l d i e r (Fig. 135). - Head subquadrate, with an incomplete disc; head dorsum slightly convex on the frons and weakly concave anterolaterally. Frontal carinae broad, slightly upturned and converging before the eyes. Vertexal angles with a short, broad, obtuse tooth. Vertex with a pair of well developed spines connected externally by a faint carina to the frontal carinae. Mandibles broad, their sides with an impressed, round, carinate protuberance. Eyes gently convex.

Mesosoma broad anteriorly, narrowing posteriorly. Pronotum with the anterior border convex; its sides with a pair of developed, bidentate, rectangular lamellae converging posteriorly. Pronotal carina well developed, raised and interrupted medially by an impression. Promesonotal suture weakly impressed. Mesonotum with a pair of short, pointed, lateral tooth. Propodeal suture deeply impressed. Propodeum sloping backwards and concave posteriorly, with slightly differentiated basal and declivous faces; propodeal sides with a pair of triangular or obtuse, broad, lamellaceous teeth anteriorly, with a thin and narrow lamella medially (absent in some specimens) and with a broad lamella posteriorly. Petiole slightly narrower than postpetiole; its anterior border with a median concavity, its dorsum sloping anteriorly. Petiolar spines curved backwards, pointed, their sides not continuous with the anterior border of the petiole. Postpetiolar node convex, with a superficial concavity in the middle; postpetiolar spines curved, pointed, with the apices pointing backwards.

Gaster oval and with an anterolateral lamella not surpassing the first stigma posteriorly.

Hind femora with a pair of denticles in the middle; mid and hind basitarsi laterally compressed, with the basal part slightly broader than the distal one.

Sculpture. Head dorsum superficially reticulate and with foveae as broad as their interspaces. Foveae on the head dorsum larger and deeper posteriorly, small and shallow anteriorly. Mesosoma reticulate, with foveae larger and deeper than on the posterior half of the head dorsum, the foveae more oval and denser on the propodeum and on the abdominal pedicel. Declivous face of the propodeum reticulate only. Sides of the mesosoma reticulate, with sparse foveae on the propleurae, with dense, oval foveae on the posterior half of the mesopleurae and on the centre of the metapleurae. First gastral tergite reticulate and superimposed with superficial piligerous foveae. Corresponding sternite reticulate and slightly shining in the middle. Legs as in the worker.

Pilosity. As in the worker.

Colour. Black. Frontal carinae, apex of the last funicular joint, lamellae of the vertexal angles, lamellae of the mesosoma, petiolar and postpetiolar spines and crest of the gaster orange. Extensor face of the tibiae and tarsomeres ferrugineous. Gaster with a dark yellow pair of anterolateral spots.

Measurements (in mm) and indices: TL 7.12–7.88; HL 1.64–1.82; HW 2.14–2.44; EL 0.40–0.42; PW 2.00–2.32; PeW 0.86–1.00; PpW 0.98–1.20; HBaL 0.66–0.68; HBaW 0.19–0.20; CI 130.5–134.1; PI 105.2–107.0; PPeI 232.0–232.5; PPpI 193.3–204.1; HBaI 28.8–29.4.

G y n e (previously undescribed). - Head subquadrate with an incomplete disc, slightly convex in the middle and little concave on the sides. Frontal carinae expanded anteriorly and straight posteriorly up to the vertexal angles. Vertexal angles with a broad, obtuse, lamellaceous tooth. Vertex bearing a pair of developed teeth connected laterally by a faint carina to the frontal carinae. Mandibles with a thick lateral carina.

Mesosoma: humeral angles with a broad, pointed, lamellaceous tooth. Pronotal carina with short crenulations, impressed on the sides and interrupted on the middle by a superficial sulcus. Mesonotum and scutellum flat in side view. Lower mesopleural side with an obtuse tooth. Basal face of the propodeum short, its middle almost on the same plane as the middle of the declivous face. Sides of the basal face of the propodeum irregularly convex, converging backwards. Declivous face of the propodeum converging posteriorly.

Petiole declivous in the middle, its anterior border concave; its sides moderately convex. Postpetiole broadly convex dorsally; sides of the postpetiole with a broad, almost round, anterior tumulus.

Gaster marginate up to the stigma, not strongly protruding anteriorly.

Legs. Fore coxae angulate. Mid and hind femora not angulate. Mid and hind basitarsi slightly compressed laterally; their proximal part slightly broader than the distal one.

Sculpture. Body faintly reticulate-punctate with small foveae with interspaces smaller than their maximum diameter, dense on the pronotal sides, on the propodeum, on the sides of the lower mesopleurae, on the upper mesopleurae, on the petiolar sides and on the postpetiole; sparser on the frontal carinae, on the middle of the ventral part of the head, on the pro- and metapleurae, rare on the centre of the pronotum, on the middle of the lower part of the mesopleura and on the declivous part of the petiole. Declivous face of the propodeum, legs and gaster superficially reticulate-punctate, slightly more impressed on the anterior third and on the sides of the first gastral sternite. Gastral dorsum with relatively dense, oval, superficial foveae. Outer face of the femora and tibiae covered by deeper foveae than those on the gaster.

Pilosity. Each fovea bears a thick, appressed, canaliculate hair, denser on the cheeks, on the propodeal dorsum, on the pedicel, on the upper part of the mesopleurae and on the outer face of the tibiae, similar hairs but thinner in the gastral foveae. Rare, slightly clavate, suberect hairs, independent from the foveae on most body parts, sparser and longer on the apex of the gaster.

Colour. Black. Frontal carinae, vertexal angles, pronotal carina, humeral angles, tarsomeres, ferrugineous. Anterolateral part of the first gastral tergite with a pair of broad, yellow spots reaching the stigma.

Measurements (in mm) and indices: TL 11.34; HL 2.00; HW 2.40; EL 0.52; PW 2.56; PeW 0.92; PpW 1.16; HBaL 0.84; HBaW 0.28; CI 120.0; PI 93.7; PPeI 278.3; PPpI 220.7; HBaI 33.3.

M a l e (previously undescribed). - Head (eyes included and mandibles excluded) about 1/3 broader than long; vertexal margin straight and ending laterally in an almost round angle. Ocelli protuberant from the convex vertex. Eyes broadly convex and placed in the middle of the sides of the head. Frontal carinae diverging backwards and not reaching the posterior border of the eyes. Frons flat and separate from the clypeus by a superficial furrow. Clypeus slightly convex. Mandibles slender, laterally carinate. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view broadening backwards, superficially carinate on the sides; mesonotum convex; median Mayrian carina and parapsidial furrows weakly impressed; scutellum convex, its sides converging posteriorly; propodeum with differentiated basal and declivous faces; basal face convex, its sides converging posteriorly towards the declivous face, the latter laterally carinate.

Petiole slightly narrower than the postpetiole and with a deeply concave anterior border; petiolar sides convex medially. Postpetiole little convex dorsally; postpetiolar sides with a small, obtuse denticle in the middle.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 126.

Wings: fore wings with *R+Sc* superficially connected to a marked pterostigma. *2r* marked, *Rsf5* connected with *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; *CuA*, *M* and distal part of *1A* vestigial.

Sculpture. The whole body reticulate-punctate. Head dorsum with small, sparse foveae; the same type of foveae but larger on the pronotum, on the mesonotum and on the scutellum. Periocular area with transversal, thin rugosities. Ventral face of the head with anastomosing foveae. Propodeum and lower metapleurae with longitudinal rugosities. Pro-, meso-, and upper metapleurae with superficial, sparse foveae. First gastral segment with the reticulation less impressed than on the head and mesosoma. Remaining gastral segments and legs faintly reticulate and almost shining.

Pilosity. Head and mesosoma covered by dense, long, partly pointed and partly truncate, suberect hairs; the same type of hairs but sparser and subdecumbent on the pedicel and on the gaster. Funiculi densely covered by thin, short, decumbent hairs; similar but thinner, sparser and longer hairs on the legs and on the gaster.

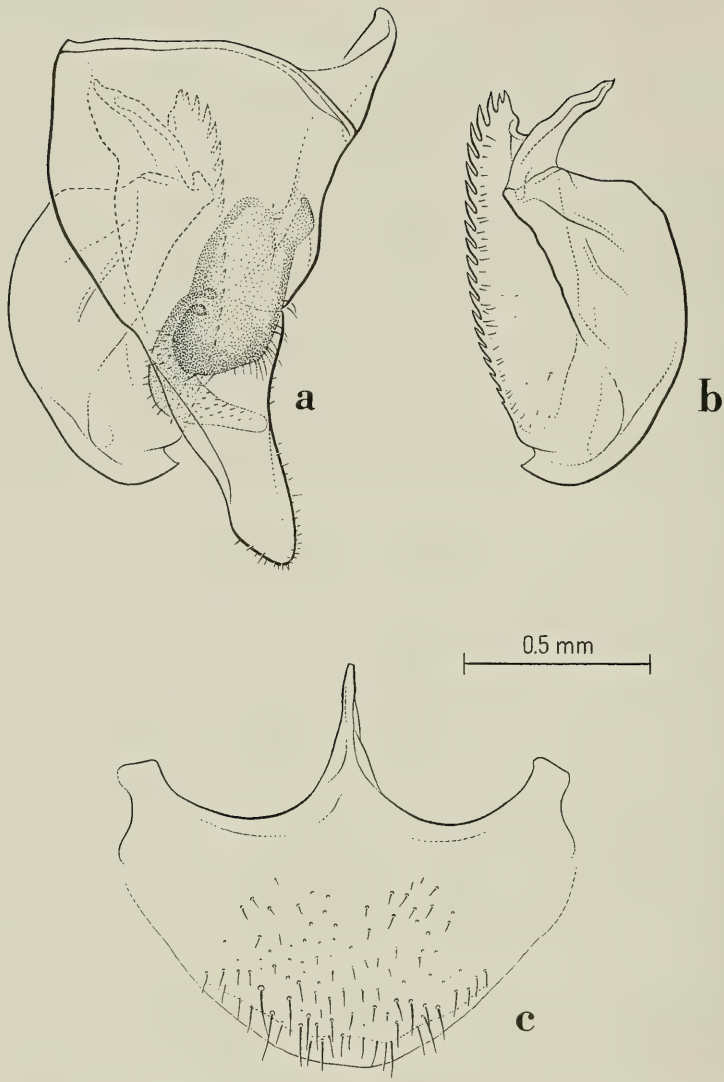


Fig. 136. *Cephalotes multispinosus* (NORTON). Male from Uxmal (Yucatan), Mexico. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Colour. Head and mesosoma black, pedicel lighter, mandibles, coxae and gaster reddish-brown. Antennae and legs yellow-orange. Wings yellowish infuscate.

Measurements (in mm) and indices: TL 6.80–7.02; HL 1.00–1.02; HW 1.28–1.32; EL 0.48–0.52; PW 1.38–1.44; PeW 0.56–0.58; PpW 0.60–0.64; HBaL 0.78–0.80; HBaW 0.12–0.13; CI 128.0–129.4; PI 88.9–95.6; PPeI 246.4–248.3; PPpI 225.0–230.0; HBaI 15.0–16.7.

Material examined. - **Mexico**: no further locality: 1 soldier (holotype of *gibbosus*) [BMNH]; 12.IV.1896, 39 workers, 11 soldiers, TOWNSEND [USNM]; 2 soldiers [MCSN, MHNG]. Vera Cruz: Orizaba, 3 soldiers, SAUSSURE [MHNG]; same locality, 1862, 8 soldiers, BIART [MNHN]; Córdoba, 20–26.VII.1964, 6 workers, 3 soldiers, T. W.

TAYLOR [MHNG]; Tlacotalpan, 14 workers, 5 soldiers, 21.VIII.1962, D. H. JANZEN [USNM]. Yucatan: Temax, 3 workers, 1 gyne, GAUMER [MHNG, MCZC, USNM]; Uxmal, 27.VII.1953, thorn forest, 6 workers, 4 soldiers, 2 males, E. O. WILSON [MCZC]. Campeche: 6 mi NE of Campoton, 12.I.1973, 12 workers, A. B. & R. J. HAMTON [MZSP]. Tabasco: Villahermosa, X.1954, 1 worker, N. L. H. KRAUSS [USNM]; Chontalpa, 06.IV.1971, 8 workers, 3 soldiers [MZSP].

Costa Rica: Alajuela, 1 worker, ALFARO [MCSN]; Hamburg Farm, Province of Santa Clara, 9.VIII.1925, 1 worker, 2 soldiers, F. NEVERMANN [MZSP].

Discussion. - *C. multispinosus* is the sister species of *goniodontus*. It shares with *goniodontus* the propodeum with triangular, lamellaceous expansions narrowing posteriorly and the pointed peduncular spines. *C. multispinosus* can be distinguished from *goniodontus* by the sparser foveae and by the triangular propodeal expansion continuing backwards.

Fig. 135 shows a small-size soldier with pronotal carina but without cephalic disc. Larger soldiers show a clear trace of disc margination.

HUNT (1983) records this species from Barro Colorado Island, Panama from where we did not see material. Since we examined material of this species from Costa Rica the record from Panama appears plausible.

Distribution: Mexico, Costa Rica and Panama.

5.6.9. The *depressus* clade

A medium-sized clade containing eight Recent species with a broad tropical distribution. It is characterised by the following three synapomorphies: (1) worker propodeum with a pair of spines followed by a tooth (char. 43, state 1), (2) worker petiole with indistinct anterior and posterior faces (char. 50, state 2), and, (3) aedeagus internally concave (char. 126, state 2). Synapomorphies (1) and (3) appear very robust and support entirely the separation of this clade. The shape of the worker petiole appears less convincing, and we suppose that its resulting synapomorphic value may be attributed either to our imprecise coding of it or to an artifact of character optimisation. Members of this clade are the first compact group of species the soldiers of which show either an in incipient or a complete cephalic disc. All remaining 79 more terminal species of the genus, except the problematic *bruchi* the soldier of which has an incipient disc only, have completely developed cephalic discs. KEMPF (1951) intuitively recognised a "*pavonii* group" roughly similar to our *depressus* clade. The main difference between our and KEMPF's groupings of species (besides the trivial addition of new species in this paper) is our exclusion from the *depressus* clade of *multispinosus* and *biguttatus*, two species that we rank within our *multispinosus* clade, a clade very close but paraphyletic to the *depressus* clade.

Species included in the clade: *betoi*, *borgmeieri*, *cordatus*, *cristatus*, *depressus*, *eduarduli*, *palustris*, *pavonii*.

Cephalotes cordatus (SMITH) new combination

Figs. 137, 138

Cryptocerus cordatus SMITH, 1854: 220. Worker. Original description. Type locality: Santarém (Pará, Brazil). Type material: presumably lost (neither in BMNH nor in OXUM). We regard as adelphotype (i. e. a specimen originating from the same series as the type but not seen by the author of the original description, a worker in MHNG labelled as follows: first label: "Cotype" [printed], second label: "*Cryptocerus cordatus* Sm., Pará" [probable handwriting of GUÉRIN], third label: "Sp. *C. cordatus*, Sm." [handwriting of GUÉRIN], fourth label: "Coll. Forel." [printed].

Cryptocerus cordatus SMITH, EMERY, 1894 a: 202. Soldier.

Cryptocerus cordatus var. *boliviensis* SANTSCHI, 1921 b: 126. Worker and gyne. Original description. Type locality: Río Guapay (Bolivia). Type material 1 worker, 1 gyne labelled "Bolivie, Río Guapay, Lizer et Delétang" in NHMB, examined. Synonymy by KEMPF, 1951: 213.

Paracryptocerus cordatus (SMITH), KEMPF, 1951: 213. First combination in *Paracryptocerus*.

Zacryptocerus cordatus (SMITH), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *depressus* clade characterised, in the worker and in the soldier, by the pronotum with a pair of continuous, slightly convex lamellae and by the meso- and metapleurae densely covered with thick hairs, and, in the gyne, by an incomplete disc, by the mesopleurae densely covered with thick hairs and by a low pronotal crest.

W o r k e r (Fig. 137) (description of KEMPF, 1951). - "Length 5.5 mm. Black; the following ferruginous: frontal carinae, occipital lobes, lateral border of pronotal lamellae, tip of epinotal and peduncular spines.

Head broader than long, sides slightly diverging caudad. Frontal carinae distinctly crenulate, expanded and somewhat upturned above the eyes, the anterior half with projecting setulae within the notches. Lateral pronotal lamellae broad, broadest in front, anterior corner subangulate, sides scarcely convex, broadest in front, distinctly converging caudad. Mesonotum with an acute lateral tooth. Sides of epinotum with an anterior plate-like, recurved spine and a posterior, shorter, triangular tooth, usually somewhat removed forward from the posterior corner of the declivous face. anterior border of the petiole evenly rounded, including the spines, which are truncate at apex. Postpetiolar spines curving forward at base, recurved at apex, truncate. Gaster slightly elongate, cordiform."

Measurements (in mm) and indices: TL 4.80–6.04; HL 1.12–1.38; HW 1.48–1.80; EL 0.40- 0.48; PW 1.40–1.72; PeW 1.04–1.20; PpW 0.82–1.10; HBaL 0.42–0.52; HBaW 0.15–0.20; CI 127.5–136.0; PI 103.6–107.2; PPeI 134.5–150.0; PPpI 151.8–195.6; HBaI 35.7–38.8.

S o l d i e r (Fig. 138) (description of KEMPF, 1951). - "Length 7.2 mm. Black; the tibiae and tarsi fuscous-ferruginous. Head subquadrate. Anterior corners rounded, posterior corners obliquely truncate and crested. Frontal carinae crenulate, slightly upturned in front of, somewhat emarginate above, the eyes. Upper surface of head scarcely convex, very finely punctate, coarsely foveolate, subfulgid. Vertex with a median transverse bidentate crest, and a lateral oblique carina between each denticule and the sides of the head. Occiput truncate. Lower border of occiput scarcely emarginate mesally. Thorax subfulgid, finely reticulate. Shoulders vestigial. Pronotum greatly expanded at the sides, with a strong transverse crest above, notched, but scarcely interrupted mesally. Mesonotum finely, but sharply reticulate-punctate, with a blunt lateral lobe. Mesoepinotal suture impressed, slightly arcuate caudad. Basal face of epinotum with a conspicuous postero-lateral lobe, which bears an upturned tubercular tooth above on the posterior corner. Upper surface and sides of thorax rather densely foveolate. Upper half of declivous face scaled and foveolate. Petiole and postpetiole as in worker, slightly stouter. All foveolae contain a golden, scale-like hair."

Measurements (in mm) and indices: TL 7.30–8.68; HL 1.80–2.12; HW 2.28–2.56; EL 0.48–0.58; PW 2.24–2.60; PeW 1.14–1.40; PpW 1.10–1.28; HBaL 0.52–0.62; HBaW 0.25–0.27; CI 115.4–126.7; PI 92.1–103.4; PPeI 172.7–203.2; PPpI 190.0–210.0; HBaI 43.3–48.1.

G y n e . - Head subquadrate, dorsally convex and with an incomplete disc. Frontal carinae strongly crenulate, expanded anteriorly, converging posteriorly before the eyes and straight posteriorly up to the vertexal angles. Vertexal angles slightly truncate and with minutely crenulate margin. Vertex with a pair of well developed, median teeth connected each other by a superficial carina continuing laterally as a thin margin until the frontal carinae. Mandibles with a thick lateral carina.

Mesosoma. Scapular angles short but visible in dorsal view. Humeral angles with a pair of broad, obtuse, lamellaceous teeth converging posteriorly. Pronotal carina superficially marked and interrupted in the middle by a superficial impression. Mesonotum and scutellum

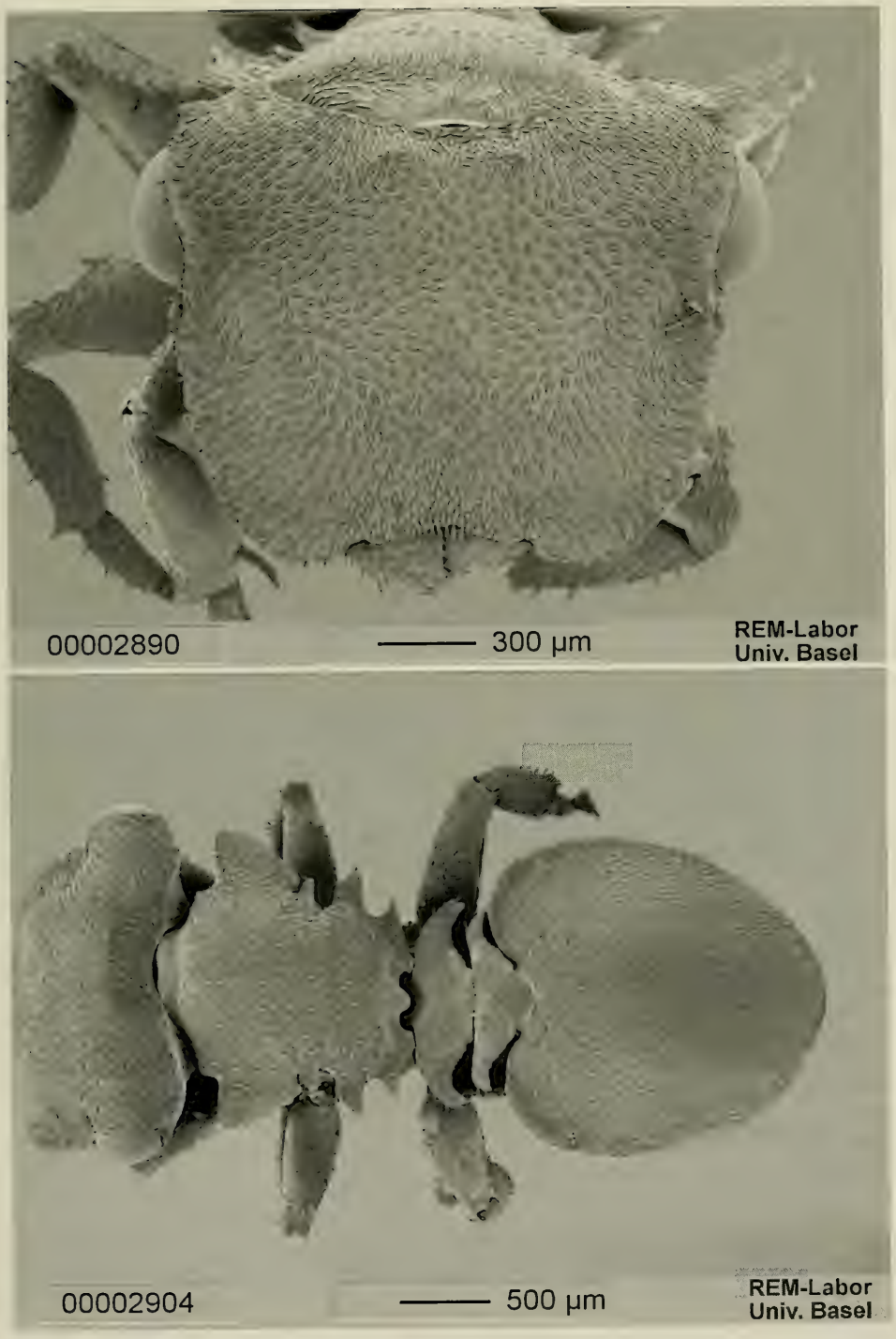


Fig. 137. *Cephalotes cordatus* (SMITH). Worker from Ilha de Marchantaria (Amazonas), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

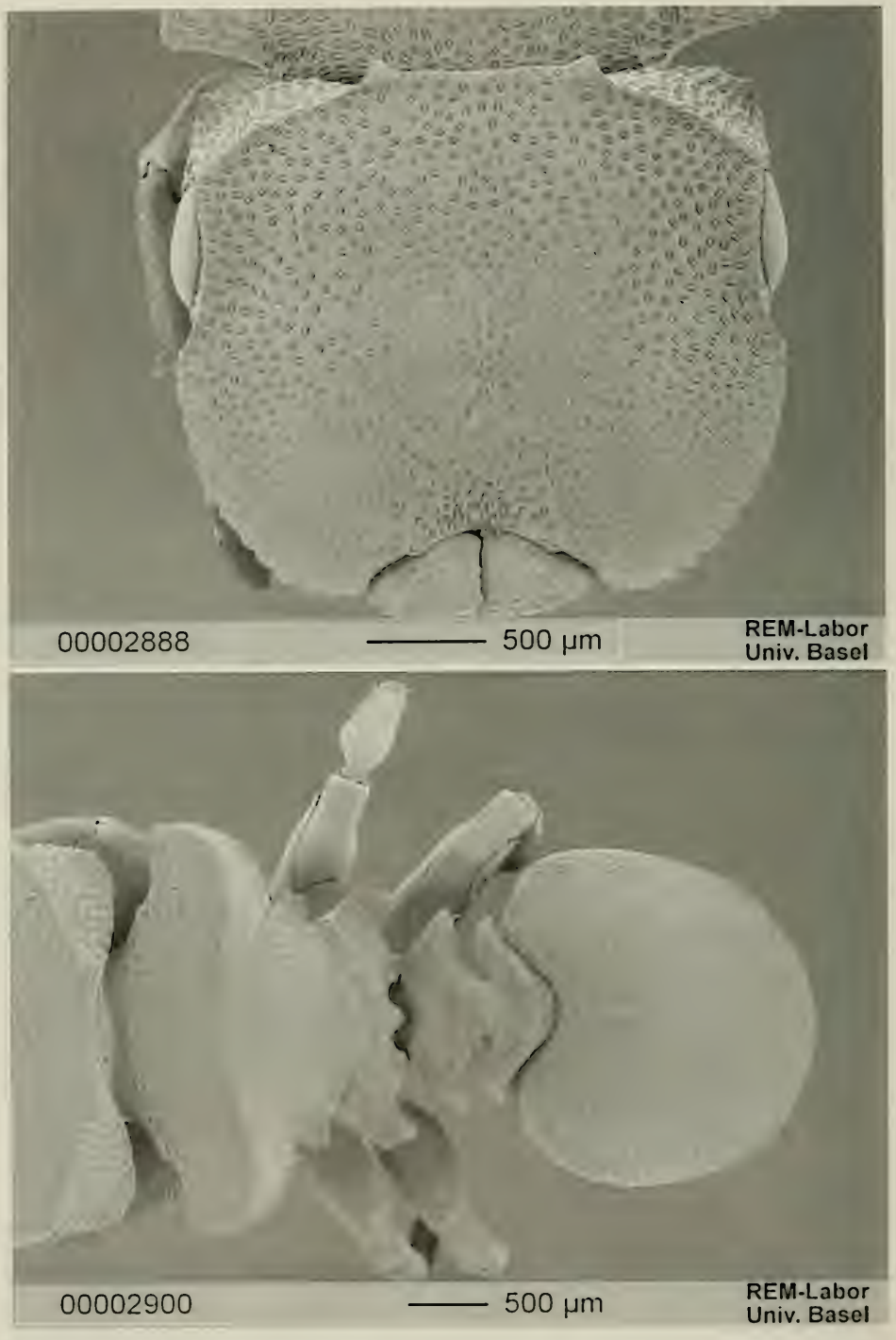


Fig. 138. *Cephalotes cordatus* (SMITH). Soldier from Ilha de Curari (Amazonas), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

flat in side view. Lower mesopleurae with an obtuse tooth. Basal face of the propodeum short. Sides of the basal face of the propodeum with two pairs of teeth subequal in size. Declivous face of the propodeum narrowing posteriorly.

Petiole with concave anterior border and anteriorly declivous dorsally; anterior half of the petiolar sides diverging into a pair of teeth, the posterior half converging posteriorly. Postpetiole broadly convex dorsally; its sides with a pair of broad spines arising from the anterior border and curved backwards.

Gaster marginate up to the stigma, slightly protruding anteriorly.

Legs. Fore coxae angulate. Hind femora angulate. Mid and hind basitarsi compressed laterally, their proximal part broader than the distal one.

Sculpture. Dorsum of the head, of the pronotum, of the mesonotum and of the scutellum minutely punctate and with small foveae variably clumped, shallower on the frontal carinae. Ventral part of the head with sculpture similar to the one on the dorsum but slightly shining and with the foveae larger and deeper. Basal face of the propodeum, pedicel and mesopleurae with oval, dense, foveae. Propleurae reticulate and with foveae on the dorsal and on the anterior thirds; propleurae with additional longitudinal, thin rugosities on the posterior half. Metapleurae reticulate and with foveae on the centre and on the anterior half of the higher part and with additional, longitudinal, thin rugosities on the ventral part. Outer face of coxae with rare, thin, rugosities, transversal on the fore coxae and longitudinal on the mid and hind coxae. Gaster and legs reticulate. Anterior and posterior thirds of the first gastral tergite, posterior half of the remaining tergites, outer face of the distal part of the femora and outer face of the tibiae with irregular, dense, superficial foveae, larger on the anterior third of the first gastral tergite.

Pilosity. Body with four types of hairs: (1) thick, appressed, originating from the foveae; (2) thinner and shorter than those originating from the foveae on the legs and on the gaster; (3) clavate, suberect on the frontal carinae, on the mesosoma, on the pedicel, on the gaster and on the legs, longer on the posterior border of the gastral tergites and sternites; (4) sparse, thin, long, slightly pointed on the gastral sternites.

Colour. Black. Frontal carinae dark ferruginous. Tibiae dark orange to ferruginous.

Measurements (in mm) and indices: TL 9.00; HL 1.68; HW 194; EL 0.49; PW 1.92; PeW 1.02; PpW 1.24; HBaL 0.60; HBaW 0.28; CI 115.5; PI 101.0; PPeI 188.2; PPpI 154.8; HBaI 46.7.

Material examined: **Colombia**: Amazonas: Leticia, VIII.1974, 1 soldier, M. L. Corn [MZSP]; same locality and collector, 04.IX.1973, 3 workers [MZSP].

French Guyana: Nouveau Chantier, 1 worker, Collection Le Moult [NHMB].

Brazil: Amapá: 19 & 23.XI.1981, 2 workers, Gorayeb et al. [MPEG]. Amazonas: Reserva Florestal A. Ducke, 2°55' S, 59°59' W, different days and months of 1981–83, 377 workers, 2 soldiers, Adis et al. [INPA]; Reserva Ducke, 09.II.1982, 1 worker, J. A. Rafael [INPA]; Ilha de Marchantaria, Rio Solimões, 59°58' W, 3°15' S, Várzea, Lago Camaleão, 01.IX.1992, 11 workers, Adis et al. [INPA]; Maraã, Rio Japurá, Ilha Jararui, 29.X–2.XI.1988, 1 worker, J. Dias [MPEG]; Itacoatiara, 1 soldier, Mann & Baker [USNM]; Ilha de Curari, Várzea, 30.IX.1976, 2 worker, 1 soldier, J. Adis [INPA]. Pará: no further locality, 1 worker (adelphotype) [MHNG]; no further locality 1 soldier, Schultz [MCSN]; Highway BR. 10, km 1712, 7.X.1980, 1 worker, W. L. Overal [MPEG]; Tucuruí, left side, 14.III.1979, 2 workers, W. L. Overal [MPEG]; same locality, I.1979, 1 soldier, M. Alvarenga [MPEG]; Santarém Novo, Fazenda Jaburu, 7–9.I.1993, 2 workers, J. Dias [MPEG]; Serra Norte, Manganês, 5–9.IX.1983, 23–26.I.1986, 2 workers, F. F. Ramos [MPEG]; São João de Pirabas, Japerica, 18–22.XII.1992, 4 workers, J. Dias [MPEG]; Chaves, Ilha Caviana, Fazenda São Luis, 15.VII & 13.VIII.1981, 1 worker, M. Fernandes [MPEG]; Conceicão do Araguaia, 28.XI.1978, 1 worker, R. B. Neto [MPEG]; Primavera, Quatipuru, Fazenda Feitoria, 28–30.XI.1992, 5 workers, J. Dias [MPEG]; Primavera, B. Vista, Ilha Arapiranga, 23–24.XI.1992, 3 workers, J. Dias [MPEG] Maranhão: São Luís, 15.I.1959, 1 worker, D. Weil [MZSP]. Piauí: 20 km S of Floriano, Buriti Sol, 5–12.XI.1991, 1 soldier, C. R. F. Brandão & P. Moutinho [MZSP]. Goiás: Gama, 19.II.1964, 1 worker, Carter [MZSP]; Jataí, XII.1972, 1 worker, F. O. M. [MZSP]. Acre: Rio Branco, 25.X–8.XI.1991, 7 workers, F. Ramos et al. [MPEG]; Porto Acre, Humaitá, 15.VI–2.VII.1992, 2 workers, Gorayeb et al.

[MPEG]. Rondônia: Alto Paraíso, 26.X–2.XI.1985, 1 worker, MZ-Polonoroeste [MZSP]; Vilhena, XI.1973, 1 worker, M. ALVARENGA [MZSP]; Rio Madeira-Mamoré, 1 worker, 1 soldier, Railroad Construction Camp 39 (284 km from Porto Velho) and Camp 41 (306 km from Porto Velho), MANN & BAKER [MCZC, USNM]; Rio Madeira, 7 workers, W. M. MANN [MCZC]. Mato Grosso: Sinop, X.1974, 1 worker, 1 soldier, M. ALVARENGA [MZSP]; Chapada, I.1960, 2 workers, C. AMANN [MZSP]; Chapada, 21.V.1972, 1 worker, R. N. WILLIAMS [MZSP]; Utiariti, 325 m, Rio Papagaio, VIII.1960, 1 soldier, K. LENKO [MZSP].

Peru: Valle Chanchamayo, 800 m, 10.VI.1958, 1 worker, WEYRAUCH [MZSP]. Junín: Satipo, 600 m, 1.8.1940, 1 soldier, WEYRAUCH [MZSP].

Bolivia: Río Guapay, 1 worker and 1 gyne (syntypes of *cordatus boliviensis*), LIZER & DELÉTANG [NHMB].

Discussion. - The specimens examined exhibit a great variation in body shape, particularly in the shape of the head and of the pronotum in dorsal view. The Amazonian specimens don't seem to differ significantly from the typical specimen from Pará in MHNG. The extremes of variation we observed can be typified by the following examples: three workers from Chapada differ from the typical *cordatus* for the gaster with thin hairs; another worker from Chapada and one from Rio Madeira, Camp. 39, differ for the pleurae with few, thick hairs; three workers from Rio Madeira, two workers from Chapada, a worker from Sinop, a worker from Reserva Ducke and a worker from Alto Paraíso, Goiás differ from the typical *cordatus* for the humeral angles more round and for the peduncular segments more broad. A worker from Gama and one from Vilhena have the vertexal angles without lamellae. The soldiers from Rio Madeira and Utiariti have the frontal carinae slightly converging over the eyes and the pronotal sides more convex. The soldiers from Reserva Florestal Ducke and Piauí have the frontal carinae slightly converging in front of the eyes and the sides of the disc weakly carinate. A soldier from Satipo (Peru) differs from typical ones for the pronotal sides more convex, for the pronotal carinae reduced, for the gaster oval and long and for the peduncular segments narrow.

We are inclined to explain these morphological differences by geographic polymorphism within a single, variable species, though we can not exclude that the collection of additional material may allow the separation of more species within what we presently regard as *cordatus*.

FERNÁNDEZ et al. (1996) report this species from the Colombian states of Caldas, Caquetá and Meta.

Distribution: Colombia, French Guyana, Brazil, Peru, Bolivia

Cephalotes palustris DE ANDRADE new species

Fig. 139

Type material: Holotype worker from Kartabo, Guyana, July-August 1920, W. M. WHEELER (MCZC); paratypes 8 workers and 1 soldier, same data as the holotype (MCZC and MZSP).

Derivatio nominis: from the Latin *palustris* (= swampy) referred to the area where this species has been collected.

Paracryptocerus pavonii (LATREILLE), KEMPF, 1951: 222, figs. 139 and 145. Worker and soldier. Nec LATREILLE, 1809. Misidentification.

Diagnosis. - A member of the *depressus* clade characterised in the worker by the vertexal angles with a pair truncate lamellae and by the mesopleurae not

densely covered with thick hairs, and, in the soldier, by the pronotal lamellae truncate and by the pronotal crest not crenulate.

W o r k e r (Fig. 139) (description of KEMPF, 1951 sub *pavonii*). - "Length 5.4 mm. Median head length 1.36 mm; Weber's length of thorax 1.58 mm. Black; the following ferruginous and subtransparent: Frontal carinae, occipital lobes, lateral projections of thorax and peduncle. Ferruginous and opaque: first funicular segment, tibiae and tarsi, except the basitarsus: Fuscous rufous: tip of mandibles, and femora. Tip of last funicular segment orange-brown.

Head broader than long: The frontal carinae distinctly crenulate and beset with projecting setulae along the anterior half. Upper surface of head rather flat anteriorly and laterad, conspicuously convex discad and caudad. Sides of head upturned above the eyes. Occipital corners with a bidenticulate lobe.

Pronotum with a broadly expanded lateral lamella, about as long as broad, broader than the length of the postpetiole, and a broad, plate-like, more or less rounded lobe, separated from the anterior lamella by a deep notch. Anterior border of the lamella convex, lateral border crenulate, posterior border concave. Mesonotum with a conspicuous spine on each side. Sides of epinotum with a large, plate-like anterior spine, and a shorter, rather slender and acute triangular tooth, arising well in front of the posterior corner of the declivous face.

Petiole broader than postpetiole, the spines plate-like, truncate at apex; the anterior border, including the spines, evenly rounded. Postpetiole with acute, apically recurved lateral spines.

Gaster emarginate antero-mesad, crested antero-laterad. About as long as broad. Sculpture and pilosity similar to that of the other species of the group".

Measurements (in mm) and indices: TL 4.96–5.72; HL 1.20–1.36; HW 1.64–1.84; EL 0.40–0.42; PW 1.76–1.92; PeW 1.12–1.28; PpW 0.96–1.08; HBaL 0.50–0.53; HBaW 0.15–0.18; CI 132.3–140.0; PI 93.2–97.9; PPeI 150.0–157.1; PPpI 172.0–183.3; HBaI 32.1- 35.5.

S o l d i e r (description of KEMPF, 1951 sub *pavonii*). - "Length 7.7 mm. Median head length 2.00 mm; Weber's length of thorax 2.17 mm. Black; the following fuscous ferruginous: anterior portion of frontal carinae, tibiae and basitarsi. Tarsi lighter.

Extremely similar to *cordatus*, from which it differs by the following characters: Pronotum without macrosculpture, smooth and fulgid. Basal face of epinotum with a broad triangular tooth on the side, the posterior border of which forms the outer border of a subequal posterior tooth; which is not upturned, nor sends out a median carinule. Declivous face finely but sharply reticulate, scales and foveolae confined to narrow band near the upper border. Anterior border of petiole not evenly curved, the slender lateral spines, pointing obliquely backward, are more or less distinctly set off from the body of the segment".

Measurements (in mm) and indices: TL 6.68–7.60; HL 1.72–1.96; HW 2.16–2.36; EL 0.45–0.48; PW 2.24–2.52; PeW 1.22–1.28; PpW 1.04–1.16; HBaL 0.50–0.60; HBaW 0.20–0.24; CI 120.4–125.6; PI 93.6–98.3; PPeI 180.6–209.0; PPpI 207.4–223.1; HBaI 40.0–41.1.

M a t e r i a l e x a m i n e d . - **Guyana**: Kartabo, July & August 1920, 9 workers (holotype and paratypes), 1 soldier (paratype), W. M. WHEELER [MCZC, MZSP].

Brazil: P a r á : Belém, APEG, 02.X.1969, 2 workers, 1 soldier, N. ROSA [MZSP]; Santarém: Taperinha, 2°54' S, 54°20' W, July, 1975, 1 worker, R. L. JEANNE [MCZC]; Aldeia Araçu, Igar. Urupi-Una, 31.I.1963, 1 worker, B. MALKIN [MZSP]; Primavera, Quatipuru, Fazenda Feitoria, 28–30.XI.1992, 1 worker, J. DIAS [MPEG]; Oriximiná, R. Trombetas, 07.X.1982, 1 soldier, A. Y. HARADA [INPA].

D i s c u s s i o n . - KEMPF (1951), without having seen Peruvian specimens, considered part of the material on which we based the description of this species to be *pavonii*, a species described from Peru the types of which have been presumably lost. The availability of Peruvian material for the present study allows the separation

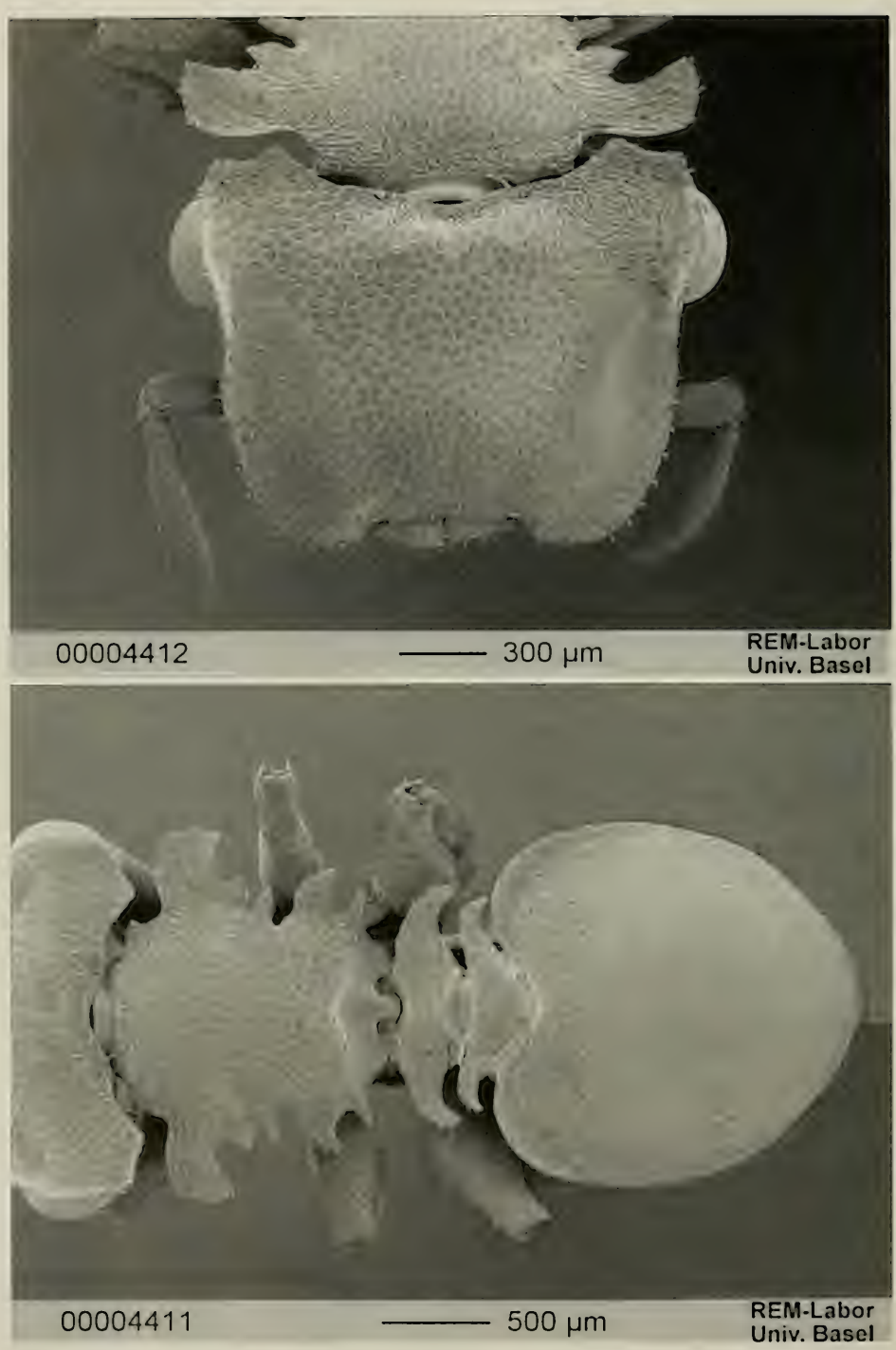


Fig. 139. *Cephalotes palustris* DE ANDRADE. Worker from Belém (Pará), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

of part of the examples from the lower basin of the Rio Amazonas from what we believe to be true *pavonii* for the characters already listed in the diagnosis.

Distribution: Guyana, Brazil.

Cephalotes pavonii (LATREILLE) new combination
Figs. 140, 141

Cryptocerus pavonii LATREILLE, 1809: 132. Worker. Original description. Type locality: S America (probably Peru). Type material: presumably lost; neotype selected for the present study, a worker from Victoria, Junín (Peru), 01.VII.1938, W. F. WALKER leg., bearing the identification label *Paracryptocerus pavonii* Latreille, det. W. W. KEMPF (MZSP); a worker, same data as the neotype (MCZC). Nec *Paracryptocerus pavonii* (LATREILLE), KEMPF, 1951: 222, figs. 139 and 145. Worker and soldier. Misidentification.

Zacryptocerus pavonii (LATREILLE), BRANDÃO, 1991: 387. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *depressus* clade characterised, in the worker, by the pronotum with a pair of long, incised lamellae, in the worker and in the soldier, by the meso- and metapleurae with rare, thick hairs, in the soldier, by the pronotal lamellae triangular, and, in the gyne, by an incomplete disc, by the mesopleurae covered with few hairs and by the pronotal crest strongly crenulate.

Worker (Fig. 140). - Head subquadrate. Vertexal angles with two pairs of teeth, the external pair small, variably pointed, the internal one large, triangular and lamellaceous. Vertex concave. Cheeks completely marginate below. Frontal carinae crenulate, broad, strongly upturned over the eyes and extending up to their posterior border backwards. Clypeal border broadly incised. Mandibles with superficial, lateral carinae. Eyes strongly convex.

Mesosoma convex in side view. Scapular angles well visible in dorsal view. Pronotal sides with broad lamellae; the lamellae directed laterally, their sides bidentate or crenulate, their posterior borders converging, with a small notch on the middle. Mesonotal teeth pointed. Propodeal suture variably impressed dorsally. Propodeum sloping backwards and slightly concave, without differentiate basal and declivous faces; its sides with a pair of spines followed by a pair of teeth, the anterior pair broad and with obtuse or pointed tip, the posterior one smaller, variably broad, and pointed. Petiole ca. 1/4 broader than postpetiole and with indistinct anterior and posterior faces. Petiolar dorsum declivous anteriorly. Anterior border of the petiole with a median concavity. Petiolar spines curved backwards, variably pointed, their sides not continuous with the anterior border of the petiole. Postpetiolar spines curved with the apices pointing backwards.

Gaster with a broad, lamellaceous anterior border reaching the first gastral stigma at least.

Hind and mid femora denticulate in the middle; mid and hind basitarsi laterally compressed.

Sculpture. Head dorsum, mesosoma and abdominal pedicel covered by reticulation and foveae, the foveae smaller and sparser on the anterior half of the head. Ventral face of the head superficially reticulate, with superimposed, anteriorly converging rugosities extending from the eyes to the submentum. Middle of the declivous face of the propodeum reticulate only. Sides of the mesosoma with longitudinal rugosities and faintly reticulate. Posterior half of the mesopleurae and middle of the metapleurae with superficial, oval foveae. First gastral tergite reticulate and with superficial foveae, the foveae denser on the anterior fourth. Corresponding sternite reticulate and slightly shining in the middle. Fore coxae reticulate and variably rugulose; mid and hind coxae with longitudinal rugosities on their extensor face. Femora and tibiae reticulate and with superficial foveae.

Pilosity. Each fovea bearing an appressed hair of size proportional to the one of the foveae. Sides of the head, of the mesosoma, peduncular segments, mandibles, legs, and gaster with short, clavate hairs. Sternites with sparse, long, suberect, truncate hairs.

Colour. Black. Frontal carinae, borders of the pronotal lamellae, tips of the propodeal and peduncular spines, gastral lamellae, tibiae and tarsi, dark orange to light brown.

Fig. 140. *Cephalotes pavonii* (LATREILLE). Worker from Sinnamary, French Guyana: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 4.12–5.30; HL 0.94–1.28; HW 1.28–1.68; EL 0.33–0.42; PW 1.34–1.76; PeW 0.84–1.08; PpW 0.68–0.84; HBaL 0.32–0.44; HBaW 0.10–0.15; CI 131.1–136.2; PI 95.4–95.5; PPeI 159.5–163.0; PPpI 197.1–209.5; HBaI 31.2–34.1.

S o l d i e r (Fig. 141) (previously undescribed). - Head subquadrate, with complete disc. Vertexal angles with two pairs of short, obtuse teeth. Head dorsum gently convex in the middle and slightly concave on the sides. Posterior border of the disc with a pair of developed median teeth connected each other by a median ridge, the ridge continuing markedly on the sides of the head into the frontal carinae. Frontal carinae with crenulate border and converging posteriorly. Mandibles broad, their sides with an impressed, round, carinate protuberance. Eyes gently convex.

Mesosoma broad anteriorly, narrowing posteriorly. Scapular angles little protuberant. Pronotal sides bearing a pair of developed, rectangular lamellae with converging sides posteriorly. Pronotal carina well impressed, raised, strongly crenulate and interrupted medially by an impression. Promesonotal suture impressed. Mesonotal sides with a pair of broad, short, obtuse or round tooth. Propodeal suture deeply impressed. Propodeum with slightly differentiated basal and declivous faces. Basal face broadening posteriorly and ending in a pair of broad, developed, rectangular, crenulate lamellae, its dorsum convex in the middle and on the same plane as the declivous face. Declivous face flat in the middle, its sides converging posteriorly and bearing medially a pair of short, triangular, lamellaceous teeth or a pair of continuos lamellae.

Petiolar node sloping anteriorly; its anterior border concave. Petiolar sides diverging posteriorly, with a median, well developed spine directed backwards. Postpetiole, in lateral view, slightly convex, dorsally gently concave; postpetiolar spines thick, arising from the anterior face and curved backwards.

Gaster suboval and with a broad anterolateral lobe, the lobe with a margin reaching the stigma.

Hind femora medially angulate. Hind basitarsi flat and with broad base.

Sculpture. Head superficially punctate and covered by large foveae broader than their interspaces, diminishing in size anteriorly. Vertexal angles and ventral sides of the head with foveae larger and deeper than those on the posterior part of the head. Centre of the ventral part of the head deeply reticulate and with sparse, small foveae. Pronotum and mesonotum reticulate and with foveae almost as broad as those on the posterior part of the head dorsum, the foveae denser on the mesonotum, on the middle and on the posterior half of the pronotum. Basal face of the propodeum, petiole and postpetiole reticulate and with dense, oval foveae. Extensor face of the femora, of the tibiae and anterior fourth of the first gastral tergite reticulate and with dense, small, oval, superficial foveae; this same sculpture but sparser to rare and superficial on the remaining gastral segments, on the pleurae and on the legs. Pleurae with thin, longitudinal rugosities. Declivous face of the propodeum reticulate only.

Pilosity. As in the worker; the short clavate hairs extend to the crenulations of the pronotal carinae.

Colour. Black, slightly shining. Frontal carinae, extensor face of the tibiae, tarsomeres, borders of the humeral angles and of the propodeal lamellae, tip of the last funicular joints and of the peduncular spines ferruginous to light brown.

Measurements (in mm) and indices: TL 6.86–7.38; HL 1.64–1.88; HW 2.06–2.28; EL 0.44–0.48; PW 2.12–2.36; PeW 1.08–1.28; PpW 0.92–1.12; HBaL 0.50–0.55; HBaW 0.17–0.20; CI 121.3–125.6; PI 96.6–98.3; PPeI 184.4–209.0; PPpI 210.7–230.4; HBaI 34.0–40.0.

G y n e (previously undescribed). - Head subquadrate, dorsally convex and with an incomplete disc. Frontal carinae strongly crenulate, expanded anteriorly, continuing straight posteriorly up to the vertexal angles. Vertexal angles slightly truncate and with two pairs of small denticles. Posterior border of the disc with a pair of well developed, median teeth connected each other by a faint carina continuing laterally until the frontal carinae. Mandibles laterally angulate.

Mesosoma. Scapular angles short but visible in dorsal view. Humeral angles with a pair of pointed spines. Pronotal sides straight. Pronotal carina marked, strongly crenulate and interrupted in the middle by a superficial depression. Mesonotum and scutellum flat in side

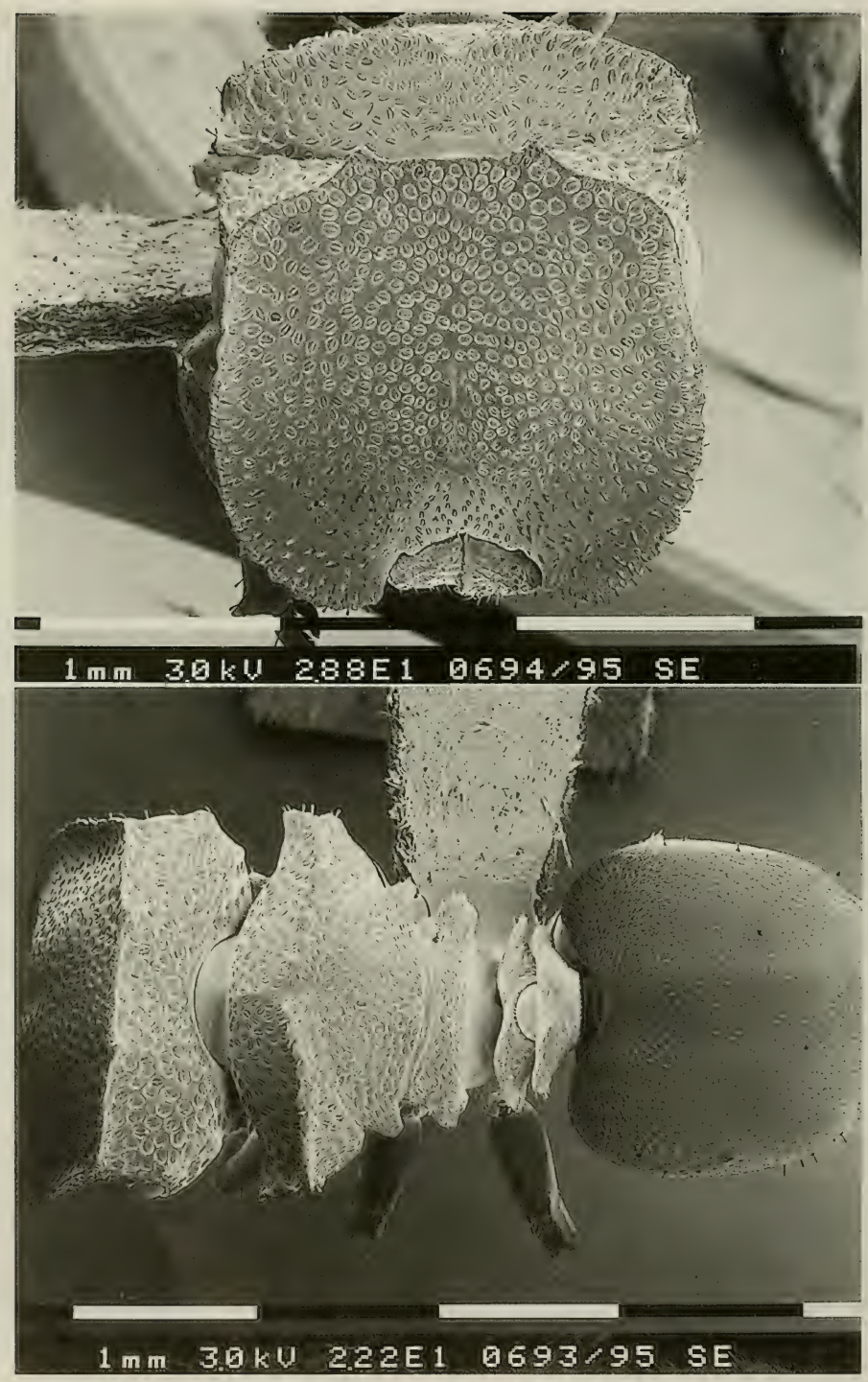


Fig. 141. *Cephalotes pavonii* (LATREILLE). Soldier from Sinnamary, French Guyana: head (top) and meso- and metasoma (bottom) in dorsal view.

view. Lower mesopleurae with an obtuse tooth. Basal face of the propodeum short. Sides of the basal face of the propodeum with two pairs of teeth of the same size. Declivous face of the propodeum with the sides converging posteriorly.

Petiole as in *cordatus*. Postpetiolar spines thinner than in *cordatus*.

Legs. Fore coxae anteriorly sharply angulate. Hind femora angulate. Mid and hind basitarsi compressed laterally, their proximal part broader than the distal one.

Sculpture. Dorsum of the head, of the pronotum, of the mesonotum and of the scutellum minutely punctate and with dense foveae, shallower on the frontal carinae, slightly larger on the pronotum. Ventral part of the head with sculpture similar to the one of the pronotum but with the punctures more impressed and with the foveae deeper. Basal face of the propodeum, pedicel and upper mesopleurae with irregular, dense, foveae. Propleurae reticulate and with foveae on the anterior third; propleurae with additional, longitudinal, thin rugosities on the posterior third. Lower mesopleurae reticulate and with foveae on the borders only; its centre with longitudinal, thin rugosities. Metapleurae reticulate and with thin, longitudinal rugosities. Outer face of the fore coxae with transversal, thin, rugosities. Outer face of the mid coxae with longitudinal, thin rugosities. Outer and posterior faces of the hind legs with longitudinal, thin rugosities. Gaster and legs reticulate. Anterior third of the first gastral tergite with irregular, superficial foveae; similar sculpture but with smaller foveae on the posterior border of the first gastral tergite, on the posterior half of the remaining tergites, on the outer face of the distal part of the femora and on the outer face of the tibiae.

Pilosity. As in *cordatus*.

Colour. Black, with mesosoma and pedicel darker, gaster lighter. Frontal carinae dark ferruginous. Tibiae and tarsi dark ferrugineous.

Measurements (in mm) and indices: TL 9.88; HL 1.88; HW 2.08; EL 0.45; PW 2.16; PeW 0.93; PpW 1.16; HBaL 0.65; HBaW 0.23; CI 110.6; PI 96.3; PPeI 232.2; PPpI 179.3; HBaI 35.4.

Material examined. - **Colombia**: Amazonas: Leticia, 70 m, VIII.1974, 1 soldier, M. L. Corn [MZSP].

Guyana: no further locality, 1970, 1 worker, N. A. Weber [USNM]. Essequibo: Essequibo R., Moraballi Creek, 13.VIII.1929, 1 worker, Oxf. Univ. Expedn. [MCZC]; Rio Essequibo, (Source), 1 worker, J. Ogilvie [MCZC].

Surinam: Nickerie: King. Fred. Wm. IV, Falls, Courantyne, 16.VII.1936, 1 worker, N. A. Weber [MCZC].

French Guyana: Cayenne: Sinnamary, Dec. 1992, 18 workers, 6 soldiers, A. Dejean [LACM].

Brazil: Roraima: Pacaraima, XII.1995, 1 worker, A. Santos [INPA]. Amapá: Amicohy, 1 soldier, L. Bicelli [MZSP]. Amazonas: Manaus, 27.VIII.1962, 1 worker, K. Lenko [MZSP]; Reserva Flor. A. Ducke, Terra firme, 2°55' S, 59°59' W, 16.III & 27.X.1982, 2 workers, Adis et al. [INPA]; Reserva Ducke, 26 km NE Manaus, 28.II.1978, 4 workers, J. Arias & N. Penny [INPA]; same locality, 22.XI.1977, 1 soldier, B. C. Ratcliffe [INPA]; same locality, 14.II.1978, 2 workers, J. Arias [INPA]; Benjamin Constant, 18–28.IX.1962, 1 worker, K. Lenko [MZSP]. Pará: Oriximiná, Ig. Jundiá, 6.X.1982, 1 worker, A. Y. Harada [INPA]; Carajás, VII-VIII.1985, UNICAMP- Ecol. Campo 1, worker, C. R. F. Brandão & W. Benson [MZSP]; São Felix de Xingu, Garimpo da Liberdade, 15–19.XI.1991, 2 workers, B. Mascarenhas [MPEG]; Serra Norte, 17.IX.1985, 1 worker, M. Zanuto [MPEG]; Serra Norte, Carajás, VII-VIII.1985, UNICAMP- Ecol. Campo 1, 2 workers, C. R. F. Brandão & W. Benson [MZSP]; Caldeirão, R. Itacaiunas, VII-VIII.1985, UNICAMP- Ecol. Campo 1, 2 workers, C. R. F. Brandão & W. Benson [MZSP]; Cachimbo, VI.1962, 1 worker, M. Alvarenga & F. M. Oliveira [MZSP]. Goiás: Jataí, XII.1972, 1 worker, F. M. Oliveira [MZSP]. Mato Grosso: Xingu, XI.1961, 1 worker, Alvarenga & Werner [MZSP]; Sinop, 55°37' W, 12°31' S, X.1974, 3 workers, M. Alvarenga [MZSP]. Bahia: Ilhéus, Itabuna, CEPEC-área Zoolog. km 22, X.1986, 2 workers, J. Delabie [MZSP]. Espírito Santo: Linhares, IX.1972, 2 workers, M. Alvarenga [MZSP]; Santa Teresa, XI.1928, 1 worker [MZSP]; Pedro Canário, Conc. da Barra, X.1972, 6 workers, M. Alvarenga [MZSP]. Rio de Janeiro: Represa Rio

Grande, Guanabara, 12–18.X.1960, 1 gyne, F. M. OLIVEIRA [MZSP]; same locality, II.1961, 1 worker, F. M. OLIVEIRA [MZSP]; Marambaia, I.1960, 2 workers, R. MÜLLER [MZSP].

Peru: Loreto: Prov. Huallaga, Río Mixiollo, 1200 m, 07.VIII.1900, 1 soldier, G. A. BAER [MNHN]. Junín: Victoria, 1.7.1938, 2 workers [MZSP] (neotype) and [MCZC], W. F. WALKER. Cuzco: Quincemil, 750 m, IX.1962, 1 worker, L. PEÑA [MCZC]. Madre de Dios: Cuzco Amazônico, 15 km NE of Puerto Maldonado, VI.1989, 1 worker, S. P. COVER & J. E. TOBIN [MCZC].

Discussion. - KEMPF (1951) regarded the specimens from Kartabo (Guyana) in the MCZC as those better fitting the original description of *pavonii* by LATREILLE (1809). As KEMPF (l. c.) noticed correctly, the Latreillean species is very likely to have been named after M. PAVON, the author of the Flora of Peru, and, as such, it is probaly based on Peruvian material. KEMPF wrote also correctly that the specimens identified as *pavonii* by most former authors actually belong to several different species. At the time of his admittedly tentative identification of the true *pavonii*, KEMPF did not see Peruvian material of this group and his identification is based solely on the very short original description. We have been able to study only two Peruvian specimens of this group. The morphology of the humeral angles of these specimens fit better than the specimens from Guyana the Latreillean diagnosis "*...thorace...ad angulos anticos producto, subcrenato*" and we consider them heterospecific from the *pavonii* of KEMPF who has much more dentate than crenate humeral angles (see the diagnosis). The specimens from Kartabo studied by KEMPF have been attributed by us to a new species (*C. palustris*, q. v.).

Since KEMPF's identification of the "true" *pavonii* is conjectural and the new, different identification we propose in this paper is also conjectural, one may argue that it would have been better to leave the things as they were. As a matter of fact, the conservative nomenclatorial solution is not without problems: the species called *pavonii* by EMERY (1890) is in part *borgmeieri* and in part *eduarduli* and the *pavonii* of FOREL (1912) is actually *C. borgmeieri*; even in the KEMPF collection, we recognise three different species under the name *pavonii* (including what we regard as true *pavonii*). By fixing a neotype from Peru we wish to be as close as possible to the truth and to prevent future uncertainties about this species.

Distribution: Colombia, Guyana, Surinam, French Guyana, Brazil, Peru.

Cephalotes cristatus (EMERY)

Figs. 142, 143, 144, 145, 146

Cryptocerus cristatus EMERY, 1890: 72. Worker, soldier and gyne. Original description. Type locality: Alajuela and Jiménez, Costa Rica. Type material: 2 workers, 1 gyne labelled "Alajuela, Alfaro" [MCSN], 3 workers and 1 gyne labelled "Costa Rica, Jiménez, Alfaro" [MCSN], 2 workers, 2 soldiers, 2 gynes labelled "Costa Rica, Alfaro" [MCSN, MHNG], examined.

Paracryptocerus cristatus (EMERY), KEMPF, 1951: 216. Partim (see var. *ruficeps* under *angustus*). First combination in *Paracryptocerus*.

Zacryptocerus cristatus, HESPENHEIDE, 1986: 395 (nec fig. 1). First combination in *Zacryptocerus*.

Cephalotes cristatus EMERY, BARONI URBANI, 1998: 325, fig. 6. Soldier and gyne. First combination in *Cephalotes*.

Diagnosis. - A member of the *depressus* clade characterised, in the worker, by the pronotum with a pair of short lamellae and by the vertex with denticles, in the soldier, by the pronotal lamellae truncate, in the soldier and in the

gyne, by the pronotal crest strongly crenulate, and, in the gyne, by the mesopleurae densely covered with thick hairs.

W o r k e r (Fig. 142) (description of KEMPF, 1951). - "Length about 5 mm. Black; the following ferruginous: frontal carinae and usually the crest on the anterolateral border of the first gastral tergite. Head slightly broader than long, the sides little diverging caudad. Frontal carinae very indistinctly crenulate, the minute projecting setulae limited to less than the anterior third. Vertex with a pair of more or less vestigial minute denticules. Occipital lobes bidentate. Thorax moderately and more or less continuously longitudinally convex. Pronotal lamellae narrower than postpetiole, longer than wide, rectangular. Behind the lamellae another short, triangular, plate-like lateral tooth, in front of the mesonotum, subequal to the lateral tooth of the mesonotum. Second epinotal spine slender, much longer than in *depressus*. Petiole with a long, recurved lateral spine arising from the anterior corner; the anterior border, including the spines, not continuously arcuate. Lateral spines of petiole curved forward at base, recurved and denticulate behind at apex. Gaster narrowly crested antero-laterad, longer than wide, its length subequal to the interocular width."

Measurements (in mm) and indices: TL 4.60–6.04; HL 1.08–1.40; HW 1.46–1.88; EL 0.40–0.45; PW 1.44–1.76; PeW 0.96–1.16; PpW 0.80–0.94; HBaL 0.48–0.56; HBaW 0.15–0.20; CI 134.3–138.2; PI 101.4–109.3; PPeI 150.0–153.5; PPpI 1.80.0–187.2; HBaI 31.2–35.7.

S o l d i e r (Fig. 143). - Head subquadrate, with complete disc; head dorsum almost flat, slightly convex on the frons and weakly concave laterally. Frontal carinae with subcrenulate border, converging posteriorly. Disc, posteriorly, with a pair of developed median teeth connected each other by a median carina continuing laterally into the frontal carinae. Vertexal corners with two pairs of short, broad, obtuse teeth. Mandibles broad, their sides with an impressed, round, carinate protuberance. Eyes gently convex.

Mesosoma broad anteriorly, narrowing posteriorly. Pronotum with the anterior border convex; its sides with a developed, rectangular, humeral angles converging posteriorly. Pronotal carina well marked, raised, strongly crenulate or denticulate and interrupted medially by an impression. Promesonotal suture impressed. Mesonotum with a broad, short, obtuse tooth. Propodeal suture deeply impressed. Propodeum with poorly differentiated basal and declivous faces. Basal face broadening posteriorly and ending in a pair of broad, strongly developed, rectangular lamellae; its dorsum convex in the middle and on the same plane as the declivous face. Declivous face flat in the middle; its sides converging posteriorly.

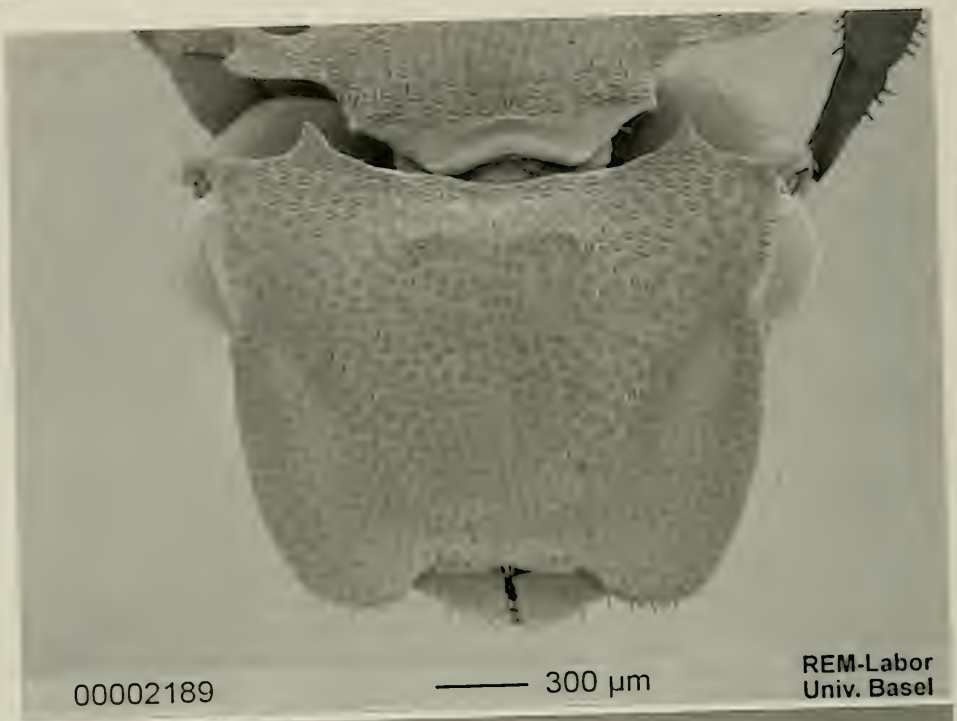
Petiole almost flat and sloping anteriorly; its anterior border anteriorly concave. Petiolar sides converging posteriorly, with a well developed spine directed backwards in their first half. Postpetiole, in lateral view, slightly convex, the middle of its dorsum gently concave; postpetiolar spines thick, arising from the anterior face of the postpetiole and curved backwards.

Gaster oval and with a broad anterolateral lobe. Anterolateral border of the first gastral sternite with a thin margin not reaching the stigma.

Hind femora medially angulate. Hind basitarsi flat and with broad base.

Sculpture. Head disc superficially reticulate and covered by small foveae almost as broad as their interspaces and diminishing in size anteriorly. Vertex, ventral face of the head and pronotum with foveae denser, deeper and larger than those on the posterior part of the head disc; the foveae are sparser in the middle of the ventral part of the head and on the propleurae. Mesonotum with the same type of sculpture as on the pronotum, but the foveae smaller and denser. Basal face of the propodeum, lower meso- and metapleurae and petiolar and postpetiolar dorsum deeply reticulate and with dense, oval foveae; the same type of sculpture but more superficial on the distal part of the extensor face of the femora and of the tibiae. Declivous face of the propodeum, upper metapleurae, legs and gaster simply reticulate. Sparse to rare foveae on the upper mesopleurae. Anterior fourth of the first gastral tergite with dense piligerous punctures, this same type of sculpture but sparser on the remaining tergite and on the anterior and posterior faces of the legs.

Pilosity. Each fovea with an appressed canaliculate hair. Legs with rare, thin, appressed hairs. Crenulations of the frontal and pronotal carinae with an erect, slightly canaliculate hair,



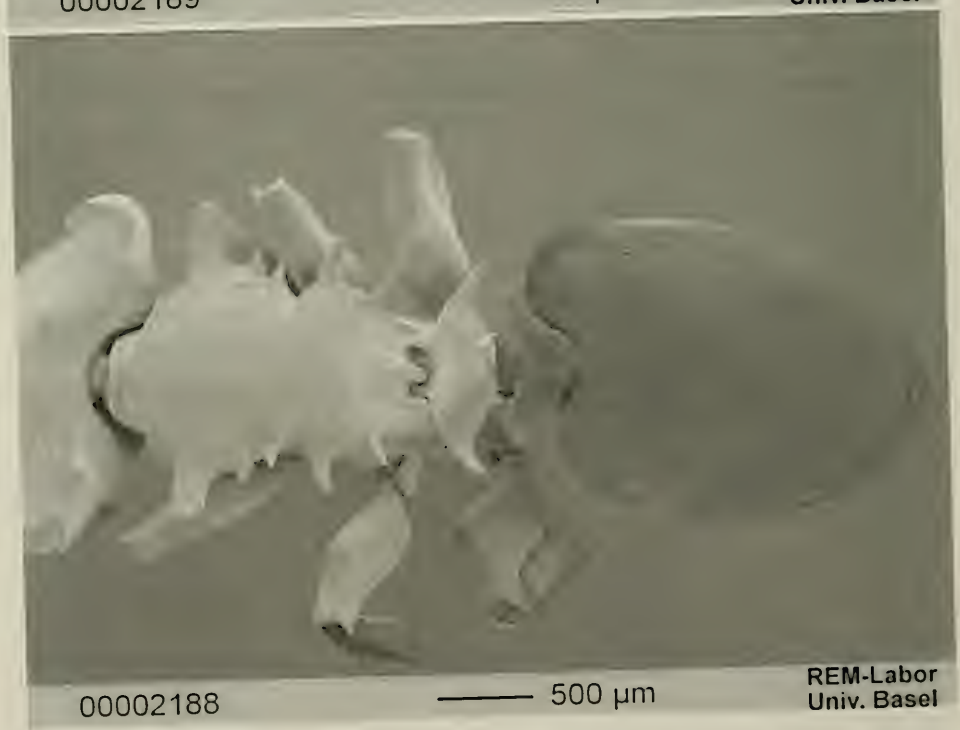


Fig. 142. *Cephalotes cristatus* (EMERY). Worker from Turrialba (Cartago), Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

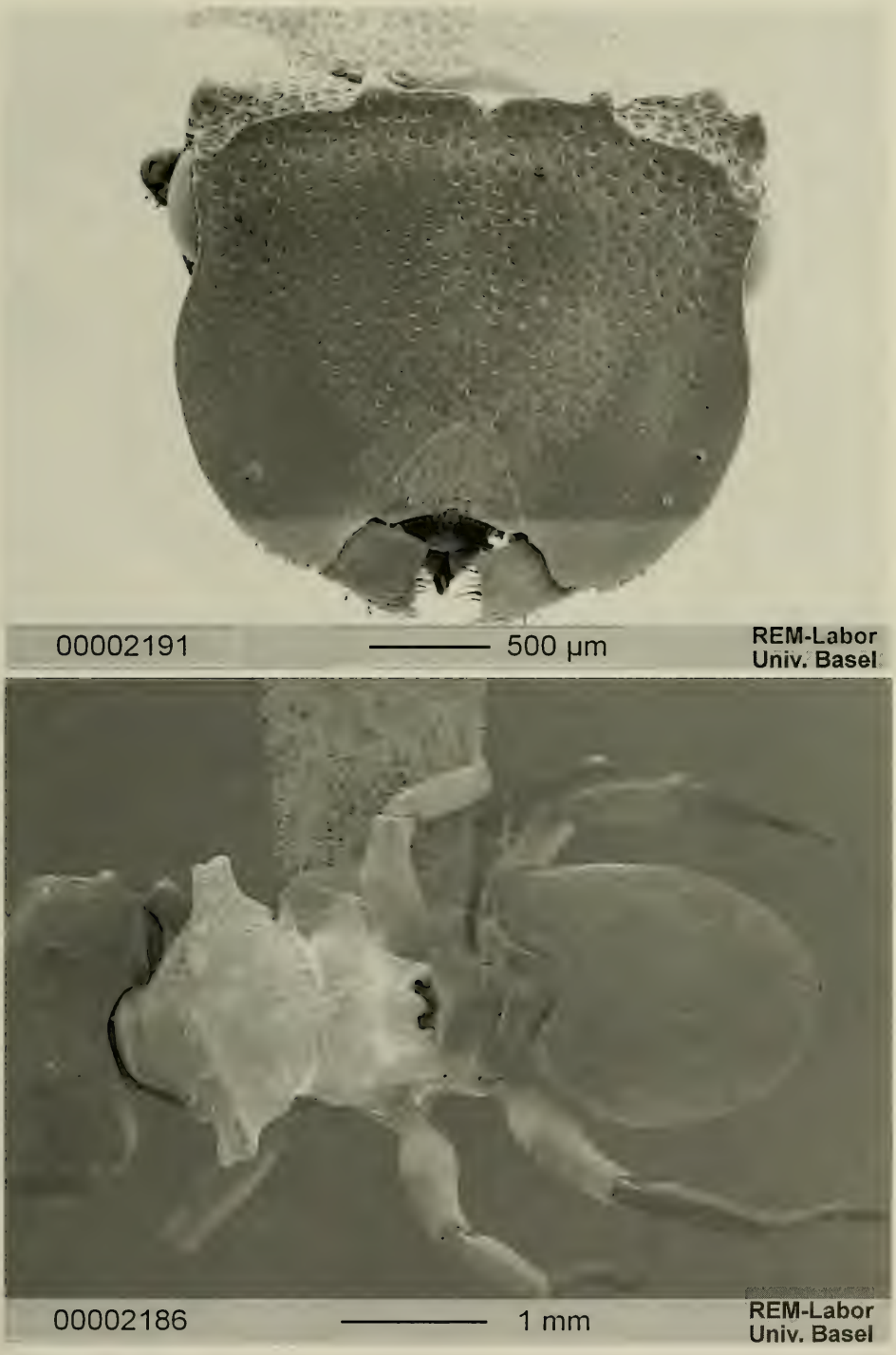


Fig. 143. *Cephalotes cristatus* (EMERY). Soldier from Turrialba (Cartago), Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

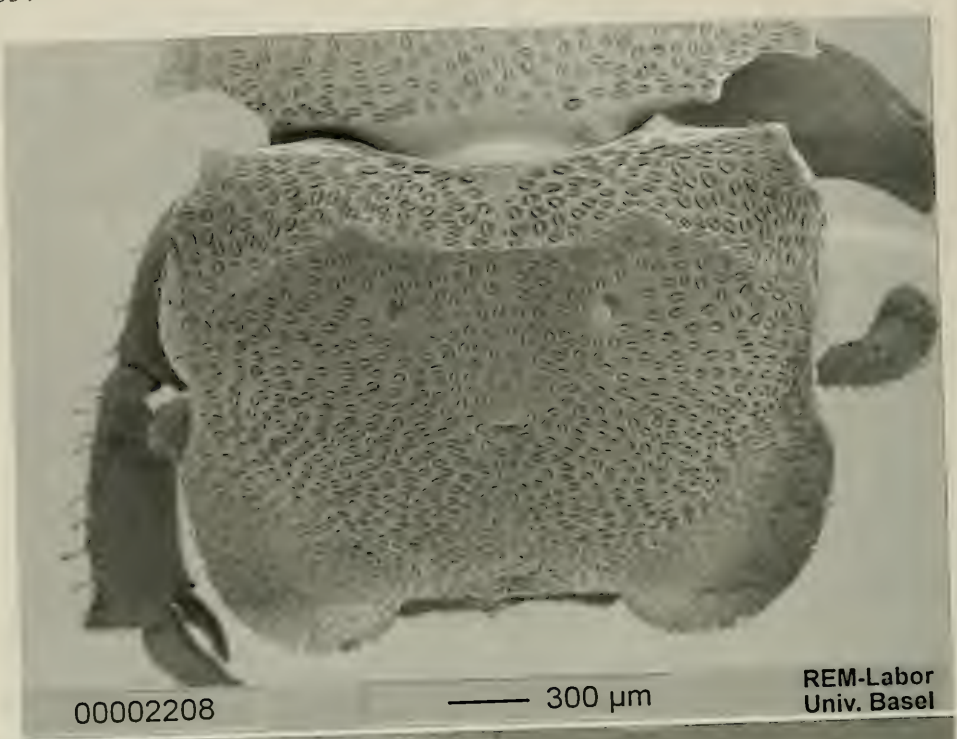


Fig. 144. *Cephalotes cristatus* (EMERY). Gyne from Colombia (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

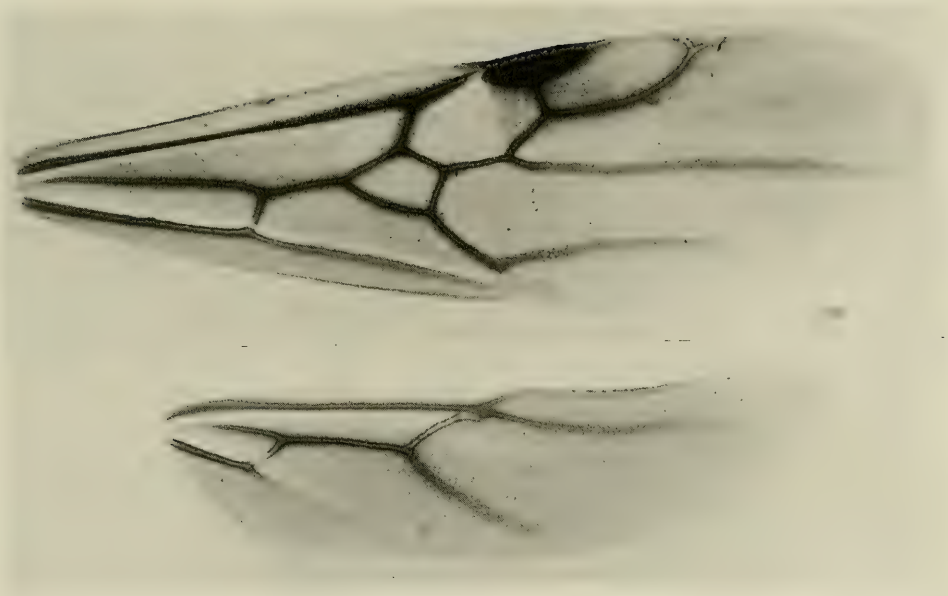


Fig. 145. *Cephalotes cristatus* (EMERY). Gyne from Colombia (no further locality), fore and hind wing.

the same type of hairs, but rarer on the sides of the thorax and of the pedicel, sparse and longer on the legs and on the gaster. Apex of the gastral sternites with sparse, long, slightly pointed hairs.

Colour. Opaque black. Frontal carinae dark ferruginous, tip of the last funicular joint and tarsomeres lighter. Head superficially shining.

Measurements (in mm) and indices: TL 7.20–7.64; HL 1.72–1.88; HW 2.24–2.40; EL 0.48–0.53; PW 2.28–2.40; PeW 1.24–1.32; PpW 1.12; HBaL 0.60–0.62-; HBaW 0.22–0.24; CI 127.6–130.2; PI 98.2–100.0; PPeI 172.7–193.5; PPpI 203.6–214.3; HBaI 35.5–40.0.

G y n e (Fig. 144) (description of KEMPF, 1951). - "Length 10 mm. Black. Head as in soldier, frontal carinae slightly less expanded, more distinctly crenulate. Vertex with a median bidentate transverse crest, the lateral carina more or less vestigial. Sides of pronotum with an acute scapular spine, pointing obliquely forward. Dorsum of pronotum with a serrated transverse crest, the median portion touching the anterior margin of the pronotum. Basal face of epinotum with a small lateral and a somewhat longer posterior tooth. Lower mesopleura with a strong tooth. Petiole less than twice as long as broad, the sides forming an obtuse stout tooth or angle, when seen from above. Postpetiole with a short conical, stout spine on each side, curving forward and recurving apically. Gaster elongate, slightly emarginate antero-mesad, distinctly marginate, not crested antero-laterad. Wings infumated, veins dark brunneous. Fore wing with a transverse cubital vein. Marginal cell closed and appendiculate."

Wings as in Fig. 145.

Measurements (in mm) and indices: TL 10.40–10.56; HL 2.00–2.12; HW 2.30–2.36; EL 0.56; PW 2.28–2.36; PeW 0.92–1.04; PpW 1.24–1.28; HBaL 0.76; HBaW 0.28; CI 111.3–115.0; PI 100.0–100.9; PPeI 226.9–247.8; PPpI 183.9–184.4; HBaI 36.8.

M a l e (previously undescribed, tentative attribution). - Head (eyes included, mandibles excluded) about 1/3 broader than long. Vertexal margin straight, carinate and ending in two broad, obtuse angles. Vertexal angles diverging towards the posterior border of the eyes.

Ocelli protuberant from the weakly convex vertex. Eyes broadly convex. Frontal carinae diverging backwards and not reaching the posterior border of the eyes. Frons flat. Clypeus weakly convex and declivous anteriorly; its anterior border straight. Mandibles slender and laterally carinate. Scapes twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum broadening backwards in dorsal view. Scapular angles distinct from the pronotal sides. Humeral angles with a pair of denticles. Pronotal sides superficially carinate. Mesonotum convex; median Mayrian carina and parapsidal furrows impressed; scutellum convex. Propodeum with slightly differentiate basal and declivous faces; basal and declivous faces converging posteriorly; basal face posteriorly declivous and unarmed.

Petiole narrower than the postpetiole and with a deeply concave anterior border; petiolar dorsum declivous anteriorly; anterior third of the petiolar sides diverging, remaining two posterior thirds strongly converging backwards. Postpetiole weakly convex dorsally; postpetiolar sides with a pair of triangular teeth, and converging posteriorly.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 146.

Wings. As in the gyne.

Sculpture. Body deeply reticulate-punctate. Head with irregular, sparse and variably marked rugosities, thicker on the posterior third and on the ventral part of the head, more regular on the periocular area, very thin on the frons; frons with additional minute foveae. Pronotum, mesonotum and scutellum with irregular foveae, absent on the centre of the pronotum. Basal face of the propodeum with longitudinal rugosities reaching the anterior half of the declivous face. Pleurae with rugosities, longitudinal on the lower pro- and metapleurae, irregular on the mesopleurae and upper metapleurae, absent on the upper propleurae. Mesopleurae with additional, irregular foveae. Pedicel, gaster and legs superficially reticulate-punctate, the punctures more impressed on the tibiae.

Pilosity. Head and mesosoma covered by dense, long, suberect hairs, sparser and subdecumbent on the pedicel, on the sternites and on the legs, rare on the tergites. Funiculi densely covered by thin, short, decumbent hairs; similar but thinner, sparser and slightly longer hairs on the legs and on the gaster.

Colour. Dark brown to black. Scapes, gaster and legs light brown.

Measurements (in mm) and indices: TL 5.42; HL 0.92; HW 1.28; EL 0.44; PW 1.12; PeW 0.51; PpW 0.63; HBaL 0.73; HBaW 0.14; CI 139.1; PI 114.3; PPeI 219.3; PPpI 203.2; HBaI 19.2.

Material examined. - **Mexico**: plant material from Huachinango, Puebla, 07.II.1945, 3 workers, 1 gyne (intercepted at El Paso, Texas by U. S. Plant Quarantine Inspectors), R. R. Juares [MZSP]; on Bamboo from Mexico, 19.II.1945, 1 male (intercepted at El Paso, Texas by U. S. Plant Quarantine Inspectors) [USNM]. San Luís Potosi: 3 mi east of Xilitla, 10.I.1952, in hollow stem, 2 workers, 1 soldier, Creighton [MZSP]. Vera Cruz: Las Hamacas, 17 km near Santiago, Tuxtla, 26–28.VIII.1953, trop. everg. for., 9 workers, 3 soldiers, 1 gyne, E. O. Wilson [MCZC, MZSP]; Córdoba, 03.V.1908, 1 worker [USNM]. Chiapas: Ococingo, Laguna Ocotal Grande, ca. 950 m, 20.VII–1.VIII.1954, 1 soldier, R. L. Dressler [MCZC].

Belize: no further locality, 1 worker, 3 gynes [MCZC, USNM]; nr. Belize, 2 workers, VIII.1959, N. L. H. Krauss [USNM]; near Macal River, 10 mi S Augustine, VII/1963, 1 worker, Reiskind [MCZC].

Guatemala: Trece Aguas, Alta V. Paz, 27.IV, 1 worker, in cacao, Schwarz & Barber [MCZC].

Honduras: Prieta, 05.IV.1924, 1 worker [MCZC]; Lago Yojoa, N end, steep forest slope, 700 m, rot wood, Mar. 1979, 2 workers, W. L. Brown [MCZC].

Costa Rica: no further locality, 1 worker, 2 soldiers, 2 gynes, (all syntypes), Alfaro [MCSN, MHNG]; no further locality, XII.1894, 4 workers, A. Alfaro [MCSN]; no further locality, 1 gyne, F. Nevermann [MZSP]; no further locality, 3 workers, Biolley [MHNG]; no further locality, 5 workers [USNM]; no further locality, 1 gyne, P. Serre [MNHN]; Alajuela, 2 workers, 1 gyne, (syntypes) [MCSN]; Jiménez, 2 workers (syntypes), Alfaro [MCSN]; La Caja, San José, 1100 m, troncs, VIII.1904, 5 workers, 1 soldier, Biolley

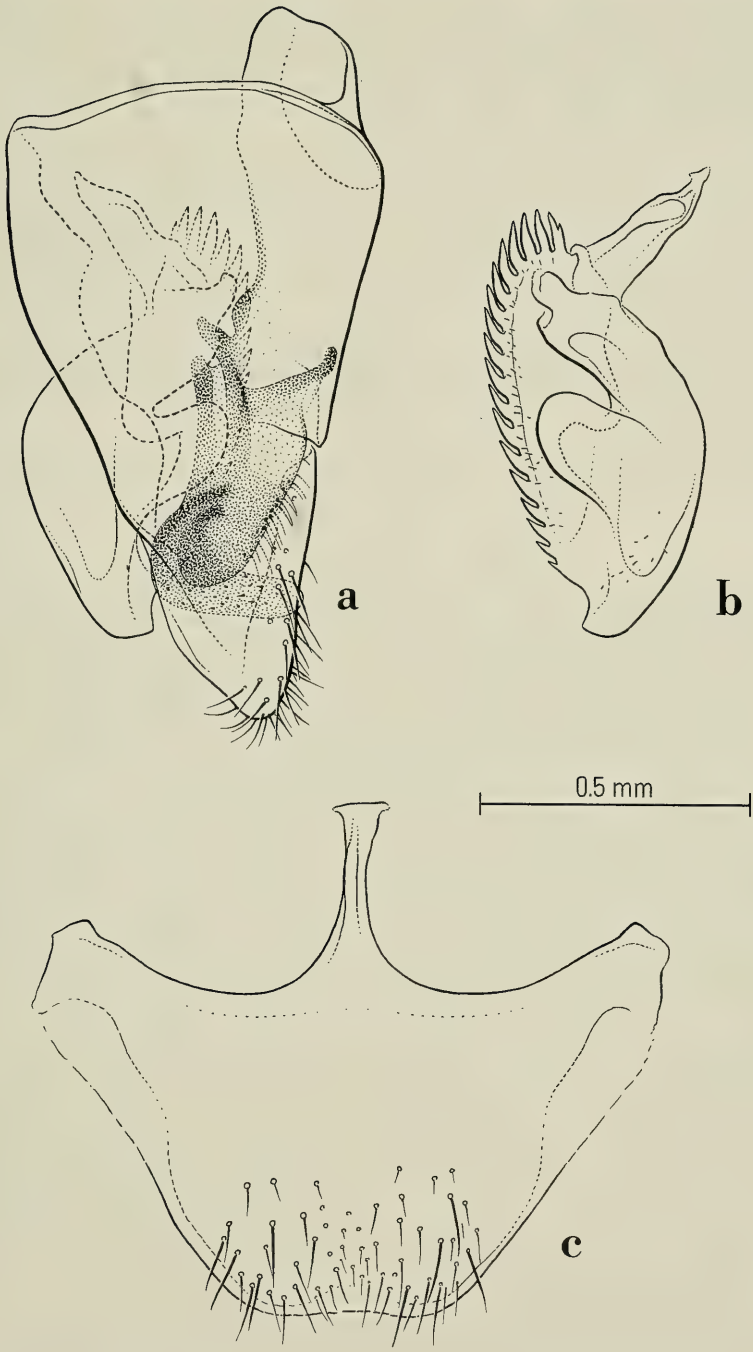


Fig. 146. *Cephalotes cristatus* (EMERY). Male from Mexico (no further locality). Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

[MHNG, NHMB]; San José, 1940, 7 workers, 6 gynes, H. SCHMIDT [MCZC, MZSP]; San José, 1.XII.1911, 6 workers [MCZC]; Cartago, Turrialba, 30–31.V.1973, 610 m, 2 workers, 1 soldier, Ginter EKIS [USNM]; Cartago, Turrialba, Volcán, 1450 m, 03.VI.1973, 1 worker, Ginter EKIS [USNM]; Turrialba, IICA, Aug. 1963, 2 workers, C. C. PORTER [MCZC].

Colombia: no further locality, 26.XII.1939, on *Cattleya*, 1 gyne [USNM]; La Esperanza, 20.VII.1936, 1 worker, R. P. ROBA [MCZC].

Discussion. - *C. cristatus* is the only species of the *depressus* clade reaching Mexico to the North and represented only by two Colombian records in South America. This Central American species shares by synapomorphy with *pavonii* the pronotal crest strongly raised and crenulate in the soldier and in the gyne.

We are rather confident on the attribution to this species of the previously undescribed male in the USNM unaccompanied by workers. Its label is very similar (though not identical) to the label of *cristatus* workers in MZSP and this is the sole known Mesoamerican species of the clade.

Distribution: Mexico, Belize, Guatemala, Honduras, Costa Rica, Colombia.

Cephalotes borgmeieri (KEMPF)
Figs. 147, 148, 149, 150, 151, 152, 367, 368, 369

Cryptocerus pavonii (LATREILLE), EMERY, 1890: 73, pl. 8, figs. 7, 10 (nec LATREILLE, 1809). Gyne, male. Misidentification declared by KEMPF, 1951: 211. Nec soldier. Vide sub *eduarduli*.

Paracryptocerus borgmeieri KEMPF, 1951: 211, fig. 147. Worker. Original description. Type locality: Iguazú (Misiones, Argentina). Type material: holotype and 3 paratype workers at the Instituto Miguel Lillo, Tucumán (Argentina) (KEMPF, 1951), not available for the present study, one paratype worker in MZSP (examined).

Paracryptocerus borgmeieri KEMPF, KEMPF, 1969: 285. Gyne.

Zacryptocerus borgmeieri KEMPF, BRANDÃO, 1991: 305. First combination in *Zacryptocerus*.

Cephalotes borgmeieri (KEMPF), BARONI URBANI, 1998: fig 5. Worker, soldier and gyne, caste polmorphism. First combination in *Cephalotes*.

Diagnosis. - A member of the *depressus* clade differing from its next in-group species, *betoi*, in the worker and in the soldier by the infuscate frontal carinae and by the pronotal lamellae truncate, and in the worker, soldier and gyne by the larger HBaI.

Worker (Figs. 147, 369) (description of KEMPF, 1951). - "Length 5.7 mm. Median head length 1.34 mm; Weber's length of thorax 1.58 mm. Fuscous reddish-brown; appendages more or less rufous-brown; gaster almost black.

Head subopaque, greatly depressed; subquadrate. Interocular distance exceeding maximum length of head. Mandibles very finely reticulate-punctate, vestigially rugulose. Frontal carinae rounded in front, slightly sinuate and subparallel at the sides, somewhat upturned above the eye, reaching the occipital corner. Sides vestigially crenulate, the projecting setulae in the notches minute to obsolete. Upper surface of head very little convex, very finely reticulate-punctate, somewhat more coarsely reticulate-rugulose, rather densely covered with large, oval, appressed, canaliculate, pale yellowish, glittering, scale-like hairs. Vertical teeth vestigial. Occipital border emarginate, occipital corners obliquely truncate, with an outer blunt and an inner more acute denticule. Cheeks strongly marginate beneath, very densely covered with minute scales as on upper surface. Lower surface with distant, longitudinal rugulae, and sparse, scattered, simple, appressed hairs.

Thorax subopaque; much broader across the pronotum than long. Upper surface of thorax including the declivous face of epinotum continuously and cospicuously convex in profile.

Sculptured and scaled as the upper surface of head. Anterior border arcuate, shoulders angulate, separate from the broad, long, lateral lamellae of the pronotum, the anterior border of which is arcuate, the outer border sinuate, the posterior border concave. Promesonotal suture obsolete. Mesonotum with a blunt lateral spine. mesoepinotal suture obsolete. Sides of epinotum with a long, plate-like depressed spine in front, and a shorter, triangular, plate-like tooth behind, close to the posterior corner, the posterior border of which forming a crest, delimiting the declivity behind. Sides of thorax finely reticulate-punctate, distinctly longitudinally rugose, with sparser, canaliculate scales, longer than those on the upper face. Mid and hind femora distinctly angulate above. Mid and hind basitarsi flattened and broadened proximad, attenuate distad.

Petiole subopaque; anterior border, including the long recurved spines, evenly curved. Postpetiole subopaque, narrower and shorter than petiole, lateral spines slightly curved forward at base, vestigially recurved at apex. Sculpture and scales as on thorax.

Gaster subopaque, cordiform, about as broad as long. First gastral tergite moderately emarginate anteriorly mesad, narrowly crested antero-laterad, sculpture and scales as on thorax."

Measurements (in mm) and indices: TL 3.96–5.96; HL 0.92–1.44; HW 1.28–2.00; EL 0.32–0.48; PW 1.28–2.04; PeW 0.90–1.40; PpW 0.72–1.08; HBaL 0.32–0.48; HBaW 0.12–0.22; CI 131.2–141.6; PI 93.3–100.0; PPeI 140.6–147.8; PPpI 1.66.6–188.9; HBaI 37.5- 45.8.

S o l d i e r (Fig. 148, 368) (previously undescribed). - Head subquadrate, with an incomplete disc. Head dorsum convex. Vertexal corners with two pairs of obtuse teeth or almost truncate. Posterior border of the disc with a pair of developed median teeth superficially connected each other by a median carina, the carina superficially continuing laterally into the frontal carinae. Anterior half of the frontal carinae with broad, crenulate border; posterior half of the frontal carinae converging before the eyes, ending on their posterior border and strongly marginate above them. Mandibles broad, their sides with an impressed, round, carinate protuberance. Eyes gently convex.

Mesosoma broad anteriorly, narrowing posteriorly. Scapular angles short but visible in dorsal view. Pronotal sides with a pair of developed, broad, rectangular lamellae; their sides converging posteriorly. Pronotal carina well marked, raised, superficially crenulate and interrupted medially by an impression. Promesonotal suture impressed. Mesonotal sides with a pair of broad, obtuse teeth. Propodeal suture deeply impressed. Propodeum with poorly differentiated basal and declivous faces. Basal face broadening posteriorly and ending in a pair of broad, thick, obtuse or round spines; its dorsum gently convex in the middle and on the same plane as the declivous face. Declivous face straight in the middle; its sides converging posteriorly and bearing medially a pair of triangular, lamellaceous teeth.

Petiolar sloping anteriorly; its anterior border medially concave. Petiolar sides gently curved posteriorly and with a broad, triangular, pointed spine with curved apex. Postpetiole, in lateral view, slightly convex, the middle of its dorsum flat; postpetiolar spines thick, arising from the anterior face of the postpetiole and curved backwards.

Gaster suboval, with anterior expansions. Anterolateral border of the first gastral sternite with a thick margin reaching the stigma.

Hind femora medially angulate. Hind basitarsi flat and with broad base.

Sculpture. Head reticulate-punctate and covered by small foveae as broad as their interspaces, diminishing in size anteriorly. Vertexal corners, ventral face of the head, sides of the pronotum and of the mesonotum with foveae larger and deeper than those on the posterior part of the head. Middle of the pronotum and of the mesonotum with foveae denser and smaller than on their sides. Propodeum, ventral part of the meso- and metapleurae, petiole, postpetiole, distal part of the extensor face of the femora and extensor face of the tibiae with dense, oval foveae. Remaining pleural parts reticulate and with thin, longitudinal rugosities. Centre of the declivous face of the propodeum reticulate only. First gastral tergite reticulate and with dense piligerous foveae on the anterior fourth. Sternite reticulate and with sparse superficial, small foveae; centre of the first gastral sternite slightly shining.

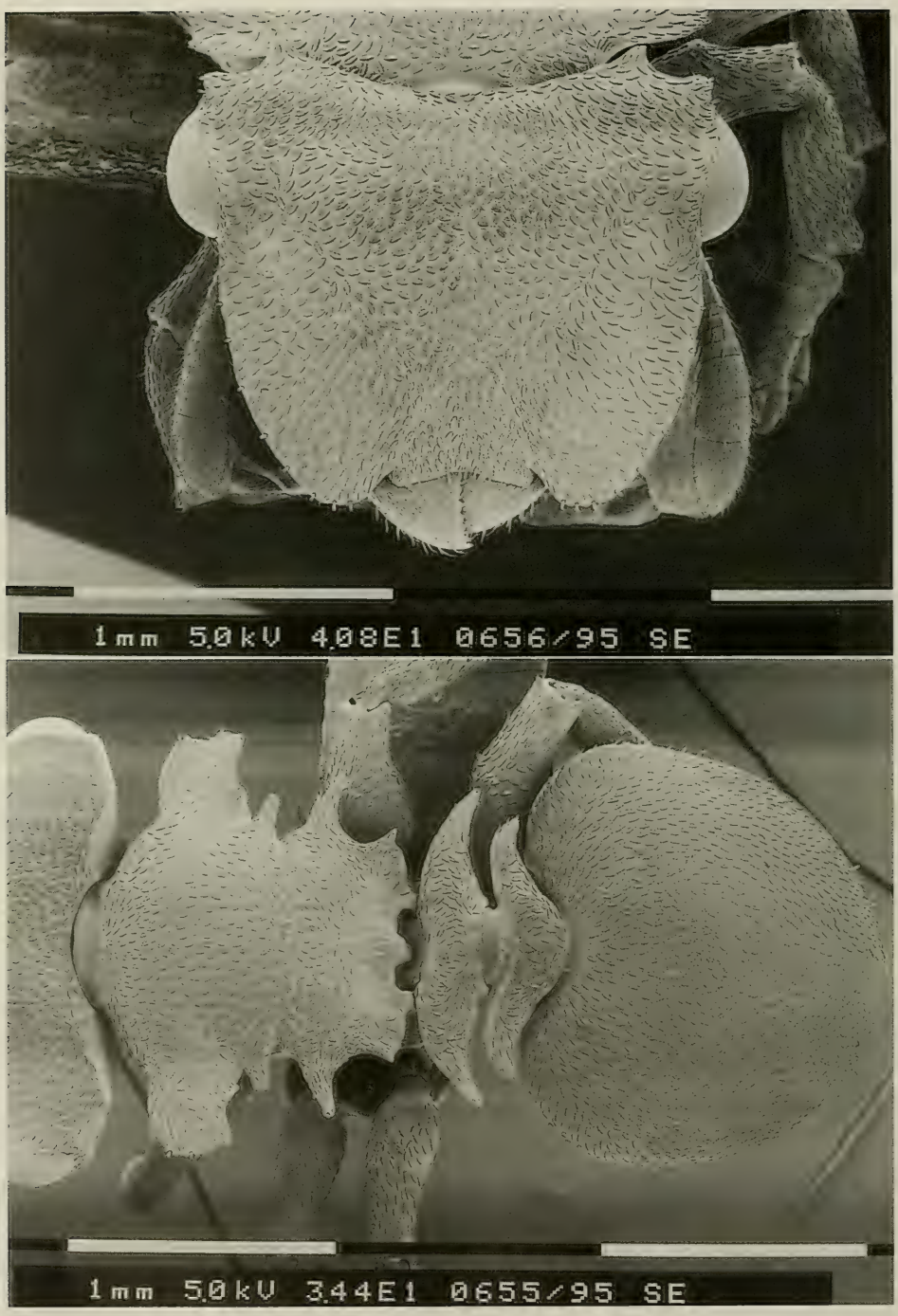


Fig. 147. *Cephalotes borgmeieri* (Kempf). Worker from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 148. *Cephalotes borgmeieri* (KEMPF). Soldier from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 149. *Cephalotes borgmeieri* (KEMPF). Gyne from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

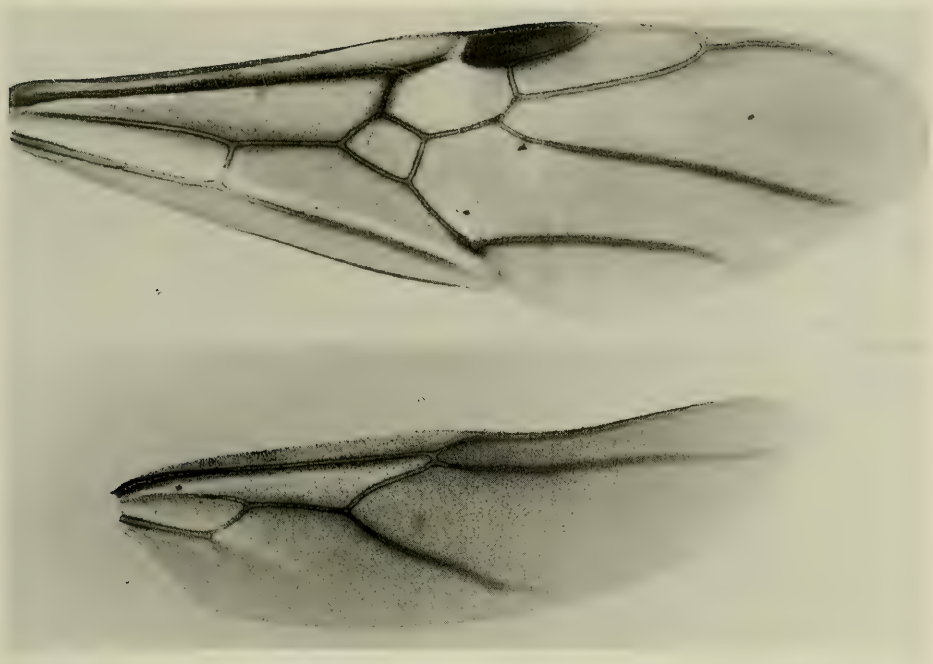


Fig. 150. *Cephalotes borgmeieri* (KEMPF). Gyne from Lins (São Paulo), Brazil, fore and hind wings.

Pilosity. Each fovea bearing an appressed hair of size proportional to the one of the foveae. Sides of the head, of the mesosoma, mandibles, legs, and gaster with sparse, short, clavate hairs. Caudal portion of the sternites with sparse, long, suberect, truncate hairs.

Colour. Dark ferruginous black. Frontal carinae and legs lighter.

Measurements (in mm) and indices: TL 7.12–8.20; HL 1.72–1.96; HW 2.32–2.52; EL 0.52–0.54; PW 2.24–2.48; PeW 1.44–1.52; PpW 1.20–1.28; HBaL 0.52–0.56; HBaW 0.24–0.27; CI 128.6–134.9; PI 100.0–103.6; PPeI 155.5–163.1; PPpI 186.7–200.0; HBaI 43.6–48.2.

G y n e (Figs. 149, 367) (description of KEMPF, 1969). - "Total length 9.6 mm; head length 2.13 mm; head width (eyes included) 2.50 mm; scape length 0.70 mm; maximum diameter of eyes 0.51 mm; thorax length 2.81 mm; maximum width of thorax 2.50 mm; petiole width 0.97 mm; postpetiole width 1.08 mm. Very close to *depressus* with the following differences: frontal carinae concolorous with rest of head; occipital corners more distinctly obliquely truncate and bidentate; occiput truncate in the middle, indistinctly marginate above the truncation, bearing on vertex, just behind the ocelli a pair of small to vestigial teeth; scapular spine stronger, more protruding, pointing obliquely laterad and cephalad; laterotergite of pronotum mostly without impressed foveolae and appressed scalelike hairs, except on anterior margin; petiole in dorsal view broader, its sides obliquely diverging caudad, the lateral spines pointing obliquely laterad and caudad; postpetiole with longer and somewhat more delicate spines."

Wings (Fig. 150). Fore wings with *R+Sc* superficially connected to a marked pterostigma. *cu-a* superficially connected with *A*. *2r* marked, *Rsf5* connected to *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* slightly marked. Hind wings with *R*, *M+CuA* and *M* marked; *1A*,*CuA*, *M* and distal part of *A* vestigial.

Measurements (in mm) and indices: TL 9.72–9.90; HL 1.80–1.84; HW 2.12–2.16; EL 0.48; PW 2.10–2.24; PeW 0.88–0.98; PpW 0.96–1.08; HBaL 0.65–0.67; HBaW 0.28–0.29; CI 117.4–117.8; PI 94.6–102.8; PPeI 228.6–238.6; PPpI 207.4–218.7; HBaI 41.8–44.6.

Fig. 151. *Cephalotes borgmeieri* (KEMPF). Male from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

M a l e (Fig. 151). - Head about 1/3 broader than long (eyes included, mandibles excluded); vertexal margin straight, faintly carinate and ending in an obtuse or pointed corner. Ocelli protuberant from the little convex vertex. Eyes broadly convex and placed in the middle of the sides of the head. Frontal carinae diverging backwards and not reaching the posterior border of the eyes. Frons flat and separate from the clypeus by a superficial furrow. Clypeus convex, its posterior half higher than the anterior one, almost truncate. Mandibles slender, laterally carinate and with a distinct apical tooth. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view broadening backwards, superficially carinate on the sides and with a slightly marked scapular angle; mesonotum convex; median Mayrian carina and parapsidal furrows weakly impressed; scutellum convex, its sides converging posteriorly; propodeum with poorly differentiate basal and declivous faces; basal face convex, its sides converging posteriorly towards the declivous face, the latter with lateral and median carinae.

Petiole slightly narrower than the postpetiole and with a deeply concave anterior border; petiolar sides convex medially. Postpetiole little convex dorsally; postpetiolar sides convex anteriorly and converging posteriorly.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 152.

Wings as in the gyne.

Sculpture. Body deeply reticulate-punctate. Head dorsum, meso- and metapleurae with irregular and variably impressed rugulae, more regular on the periocular area, on the basal face of the propodeum and on the peduncular sides. Sparse, shallow foveae on the head and on the mesosoma. First gastral segment and legs reticulate-punctate; on the remaining gastral segments the same sculpture but less impressed and the tegument is slightly shining.

Pilosity. Head and mesosoma covered by dense, long, suberect hairs, sparser and subdecumbent on the pedicel, on the sternites and on the legs, rare on the tergites. Funiculi densely covered by thin, short, decumbent hairs; similar but thinner, sparser and slightly longer hairs on the legs and on the gaster.

Colour. Black with scapes and first funicular joints lighter; remaining funicular joints ferruginous. Coxae, trochanters and proximal half of the femora light brown; remaining legs parts yellow. Wings light brown and infuscate.

Measurements (in mm) and indices: TL 6.14–6.76; HL 0.92; HW 1.28; EL 0.44–0.46; PW 1.24–1.32; PeW 0.64–0.65; PpW 0.68–0.69; HBaL 0.56–0.60; HBaW 0.12; CI 139.1; PI 97.0–103.2; PPeI 193.7–203.1; PPpI 182.3–191.3; HBaI 20.0–21.4.

M a t e r i a l e x a m i n e d . - **Brazil**: S ã o P a u l o : Mirante do Paranapanema, 07.XII.1990, 1 worker, M. L. DE ANDRADE; Mococa, 15.VIII.1990, 2 workers, M. L. DE ANDRADE [NHMB]; Guararapes, 2 workers, M. L. DE ANDRADE [NHMB]; São José do Rio Preto, R. dos Castores, 02.IV.1968, 24 workers, VIZOTTO [MZSP]; Mirassol, Fazenda B. Grande, 12.X.1972, 3 workers, J. M. DINIZ [MZSP]; Pirassununga, 24.VIII.1976, 1 worker, L. R. FONTES [MZSP]; Lins, VIII.1995, many workers, soldiers, gynes and males, M. L. DE ANDRADE [CPCC, INPA; LACM; MCZC, MNHN, USNM, ZSMC]. M a t o G r o s s o d o S u l : no further locality, 1 worker [MHNG]; Cuiabá, 5 workers, SILVESTRI [MCZC, NHMB]; same locality, 12.IX.1900, 2 workers, 1 gyne, GERMAIN [MCSN]; Três Lagoas, Fazenda Yamaguti, Córrego da Onça, VI.1964, 2 workers, 1 gyne, Exp. Dep. Zool. [MZSP]. M i n a s G e r a i s : Paraopeba, Horto, 14.I.1965, 3 workers [MZSP].

Argentina: M i s i o n e s : Iguazú, 1 worker (paratype), N. KUSNEZOV [MZSP]; Ignacio, V.1961, 1 worker, KRAUSS [USNM].

Paraguay: no further locality, 4 workers, 1 small soldier, BALZAN [MHNG, MCSN]; no further locality 1 male, BOHLS [MCSN]; Puerto Bertoni, 3 workers (erroneously labelled as paratypes by Kempf), STREMIKOV [MCZC]; A l t o P a r a n á : Pto. Stroessner, 12.X.1974, 2 workers, P. DUELLI [MZSP]; Pastoreo, 09.XII.1974, 1 worker, P. DUELLI, [MZSP].

D i s c u s s i o n . - This species has been formerly confused with *pavonii*, a species described by LATREILLE on presumably Peruvian specimens. KEMPF (1951) detected differences between what he thought to be *pavonii* and other South Ameri-

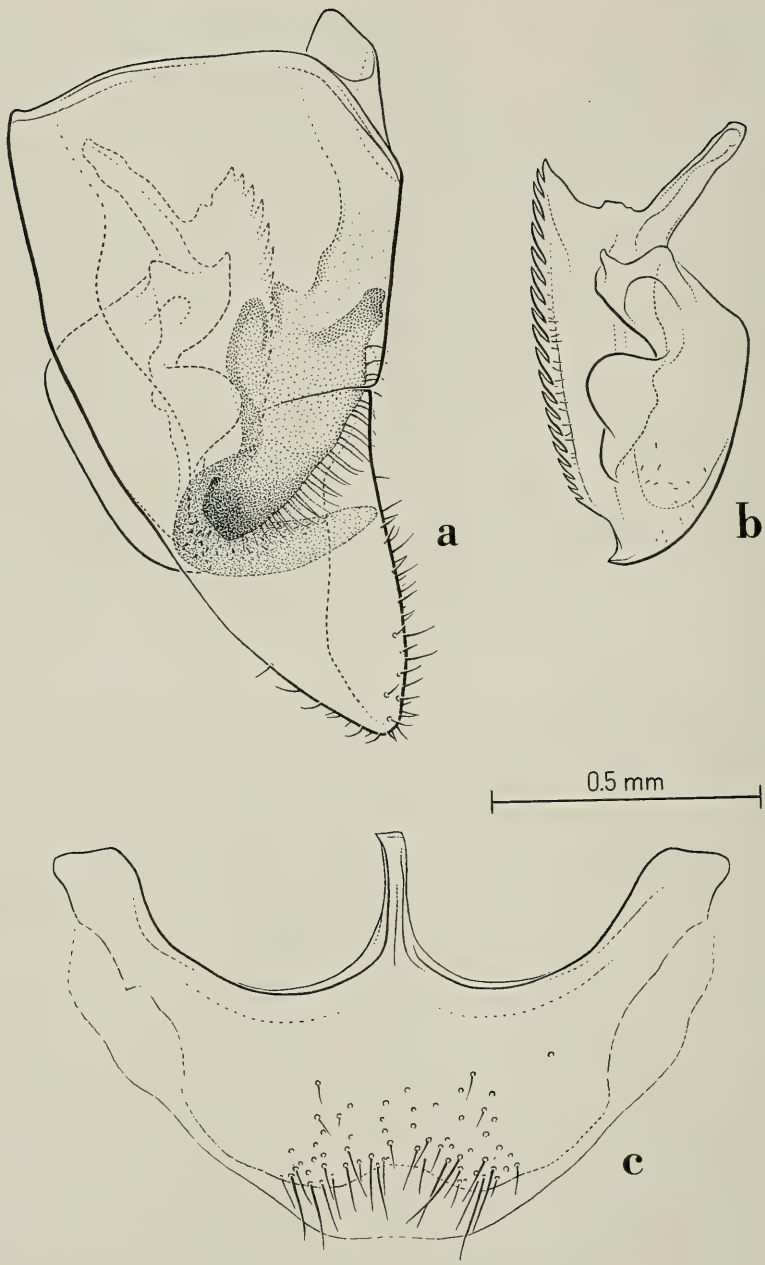


Fig. 152. *Cephalotes borgmeieri* (Kempf). Male from Lins (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

can specimens and separated the latter under the name *borgmeieri*, a species based on workers only. In his paper (l. c.) he supposed correctly that "a figure drawn and published by EMERY (1890), as the soldier of *pavonii*, represents this caste of *borgmeieri*". Later KEMPF (1958) described a soldier from Argentina which he attributed with doubt to *eduarduli*, though suspecting that it could belong to *borgmeieri*. We had the opportunity to examine this specimen together with the syntypes of *eduarduli* in the MHNG and the comparison confirms the conspecificity of the presumed *eduarduli* of KEMPF with the species described under this name by FOREL.

Distribution: Brazil, Argentina (Misiones) and Paraguay.

Cephalotes betoi DE ANDRADE n. sp.
Figs. 153, 154, 386

Type material: holotype, worker from Reserva Biológica de Águas Emendadas, Distrito Federal, Brazil, 27–30.VI.1991, C. R. F. BRANDÃO, M. L. FRANÇOSO & A. A. REIS, in MZSP; paratypes 182 workers and 12 soldiers, same data as the holotype, in MZSP.

Derivatio nominis: This species is named after "Beto", the nickname of Prof. Carlos Roberto Ferreira Brandão, the collector of most of the material on which this species is based.

Diagnosis. - A member of the *depressus* clade characterised in the worker, soldier and gyne by the pleurae and the declivous face of the propodeum with longitudinal rugosities, in the worker by the broad, long, incised pronotal lamellae and by the petiole anteriorly angulate, and, in the soldier, by the incomplete disc, by the triangular pronotal lamellae, and, in the gyne, by the absence of disc, by the fuscous frontal carinae and by the few hairs on the lower metapleurae.

Worker (Figs. 153, 386). - Head subquadrate. Vertexal corners with two pairs of teeth, the external pair small, obtuse or simply a convex margin, the internal ones large, triangular and lamellaceous. Vertex marginate and deeply concave. Cheeks completely marginate below. Frontal carinae broad, strongly upturned over the eyes and extending up to their posterior border backwards. Antennal scrobes reaching the anterior border of the eyes. Clypeal border broadly incised. Mandibles with lateral carinae; the masticatory margin with an apical and a subapical tooth followed by 0–4 denticles. Eyes strongly convex.

Mesosoma convex in side view. Scapular angles well visible in dorsal view. Pronotal sides with broad lamellae; the lamellae directed antero-laterally, their sides bidentate or crenulate, their posterior border converging, with a small notch on the middle. Mesonotal teeth pointed. Propodeal suture variably impressed dorsally. Propodeum sloping backwards and slightly concave, without differentiate basal and declivous faces; its sides with two pairs of semi-lamellaceous spines, the anterior pair broad and with obtuse tip, the posterior one smaller, variably broad, and pointed. Petiole ca. 1/4 broader than postpetiole, its anterior border with a median concavity. Petiolar spines curved backwards, variably pointed, their sides not continuous with the anterior border of the petiole. Postpetiolar spines curved with the apices pointing backwards.

Gaster with a broad lamellaceous anterior border reaching the first gastral stigma at least.

Hind and mid femora denticulate in the middle; mid and hind basitarsi laterally compressed.

Sculpture. Head dorsum, mesosoma and abdominal pedicel covered by reticulation and foveae, the foveae smaller and sparser on the anterior half of the head, on the posterior half of the propodeum and on the abdominal pedicel. Ventral face of the head reticulate, with superimposed rugosities from the eyes and converging to the submentum. Propodeum with faint, irregular rugosities on its posterior half. Sides of the mesosoma with longitudinal rugosities and reticulate. First gastral tergite reticulate and with small, superficial foveae

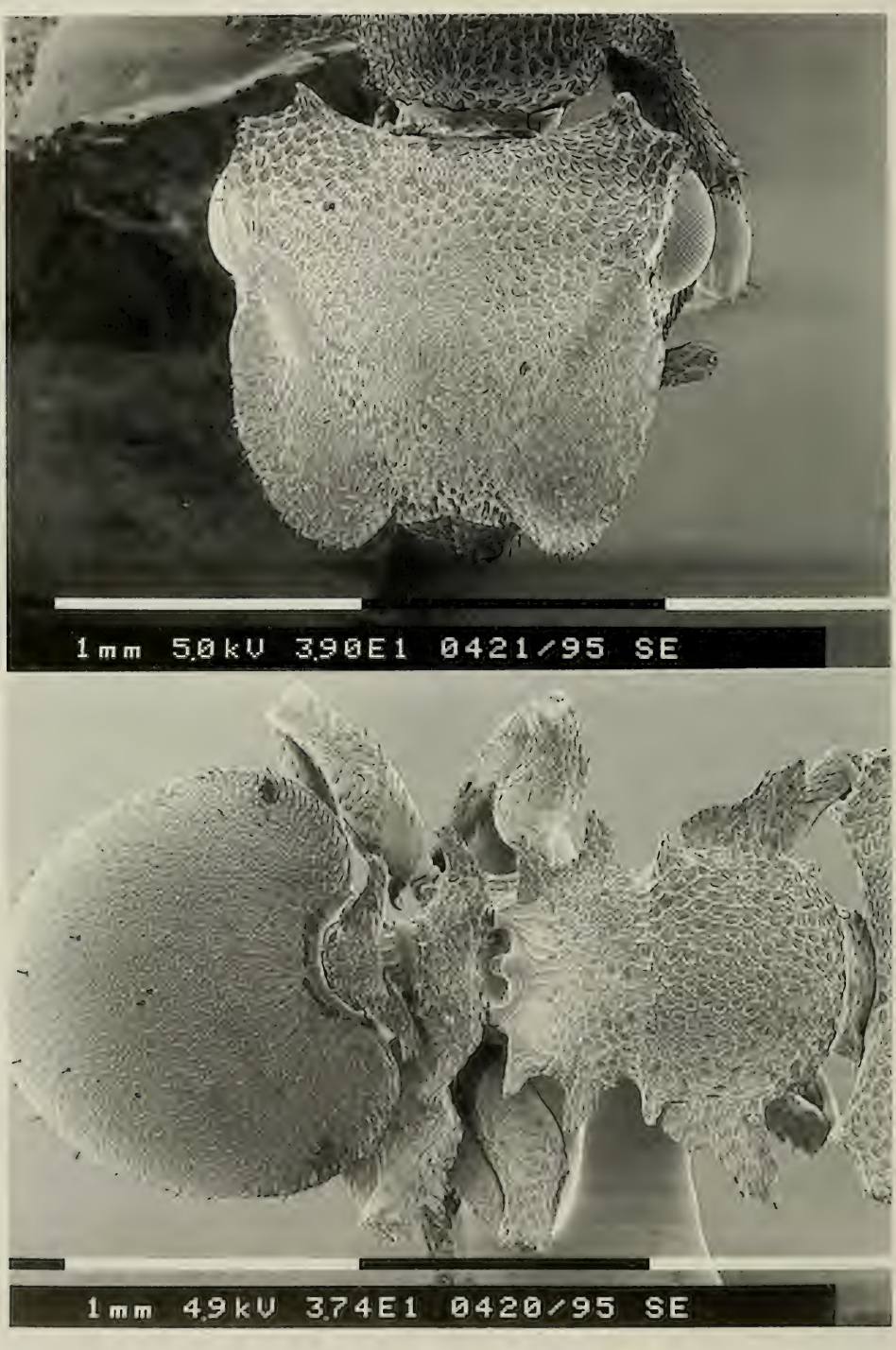


Fig. 153. *Cephalotes betoi* DE ANDRADE. Worker from Distrito Federal, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

anteriorly. Corresponding sternite reticulate and slightly shining in the middle. Fore coxae reticulate and variably rugulose; mid and hind coxae with longitudinal rugosities. Femora and tibiae reticulate and with foveae as on the anterior part of the first gastral tergite.

Pilosity. Each fovea bearing an appressed hair whose size is proportional to that of the fovea. Sides of the head, of the mesosoma, mandibles, legs, and gaster with short, clavate hairs. Sternites with sparse, long, suberect, truncate hairs.

Colour. Black. Frontal carinae, antennae, masticatory margin of the mandibles, borders of the pronotal lamellae, propodeal, and pedicular spines, gastral membranes, tibiae and tarsi, dark orange to light brown.

Measurements (in mm) and indices: TL 4.64–4.88; HL 1.08–1.16; HW 1.32–1.44; EL 0.36–0.38; PW 1.32–1.48; PeW 0.84–0.92; PpW 0.64–0.70; HBaL 0.36–0.40; HBaW 0.11–0.13; CI 122.2–127.3; PI 97.3–106.1; PPeI 153.5–160.8; PPpI 197.0–211.4; HBaI 30.5–33.3.

S o l d i e r (Fig. 154). - Head subquadrate, with an incomplete disc. Vertexal corners with two pairs of short, obtuse teeth. Head dorsum convex. Posterior border of the disc with a pair of developed median teeth connected each other by a median ridge continuing superficially on the sides of the head into the frontal carinae. Frontal carinae with crenulate border and converging posteriorly. Mandibles broad, their sides with an impressed, round, carinate protuberance. Eyes gently convex.

Mesosoma broad anteriorly, narrowing posteriorly. Scapular angles little protuberant. Pronotal sides converging posteriorly, bearing a pair of developed, triangular, humeral angles. Pronotal carina well marked, raised, strongly crenulate and interrupted medially by an impression. Promesonotal suture impressed. Mesonotal sides with a pair of broad, short, obtuse or round tooth. Propodeal suture deeply impressed. Propodeum with poorly differentiated basal and declivous faces. Basal face broadening posteriorly and ending in a pair of broad, developed, rectangular bidentate lamellae, its dorsum convex in the middle and on the same plane as the declivous face. Declivous face flat in the middle, its sides converging posteriorly and bearing medially a pair of triangular, lamellaceous teeth.

Petiolar node sloping anteriorly; its anterior border concave. Petiolar sides diverging posteriorly, with a median, well developed spine directed backwards. Postpetiole, in lateral view, slightly convex, dorsally gently concave; postpetiolar spines thick, arising from the anterior face and curved backwards.

Gaster oval and with a broad anterolateral lobe. Anterolateral border of the first gastral tergite with a thick margin reaching the stigma.

Hind femora medially angulate. Hind basitarsi flat and with broad base.

Sculpture. Head superficially punctate and covered by small, variably clumped foveae, diminishing in size anteriorly. Vertexal corners, ventral face of the head, pronotum and mesonotum with foveae larger and deeper than those on the posterior part of the head. Basal face of the propodeum, posterior half of the meso- and metapleurae, petiole, postpetiole, legs and anterior fourth of the first gastral tergite reticulate and with dense, oval foveae. Remaining pleural parts reticulate and with thin, longitudinal rugosities. Declivous face of the propodeum reticulate and with irregular, longitudinal rugosities.

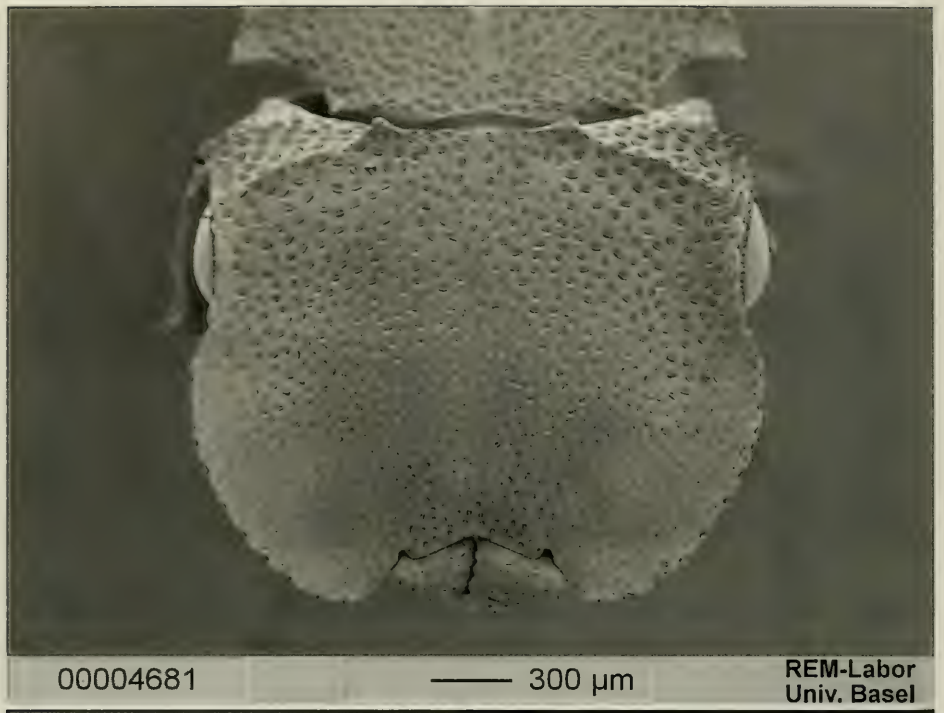
Remaining gastral tergites with small piligerous punctures; this same type of sculpture but sparser on the sternites; centre of the first gastral sternite slightly shining.

Pilosity. As in the worker.

Colour. Black. Frontal carinae dark ferruginous, tarsomeres, tip of the last funicular joints, of the humeral angles, and of the peduncular segments ferruginous.

Measurements (in mm) and indices: TL 6.36–7.32; HL 1.56–1.80; HW 1.96–2.26; EL 0.44–0.48; PW 1.92–2.24; PeW 0.96- 1.10; PpW 0.78–0.92; HBaL 0.44–0.50; HBaW 0.17–0.20; CI 125.0–125.6; PI 98.2–100.9; PPeI 200.0–215.4; PPpI 243.5–266.6; HBaI 36.0–40.0.

G y n e . - Head subquadrate, dorsally convex. Frontal carinae crenulate, expanded anteriorly, converging posteriorly before the eyes, upturned above them and gently diverging posteriorly to the vertexal angles. Vertexal angles externally with a pair of minute denticles and internally with a pair of broad, obtuse teeth. Vertex bearing a pair of dorsal denticles. Mandibles with a thick lateral carina.



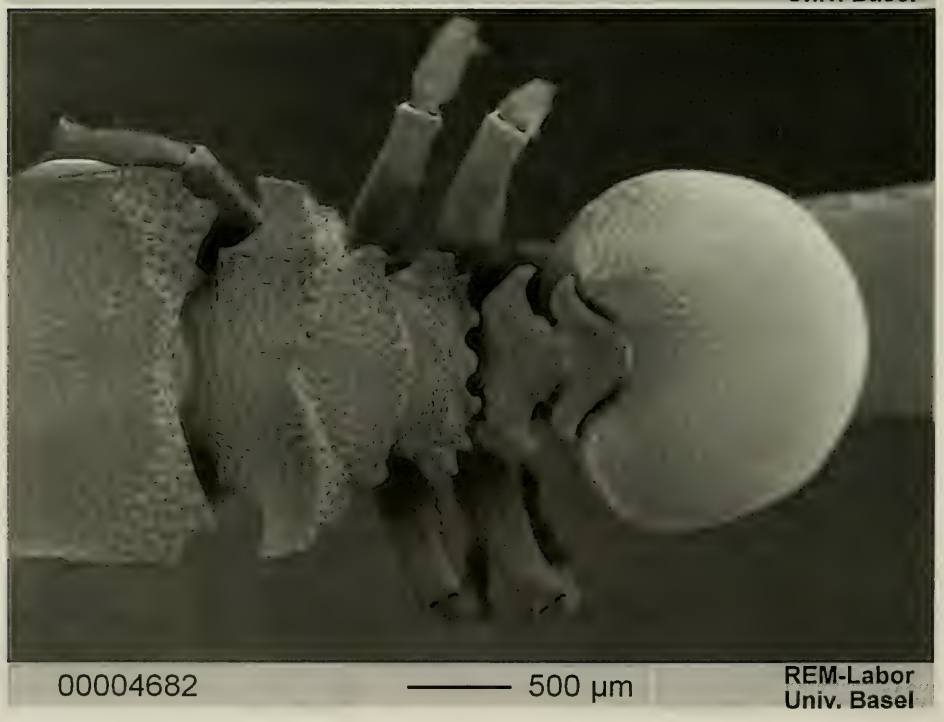


Fig. 154. *Cephalotes betoi* DE ANDRADE. Soldier from Distrito Federal, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Mesosoma. Scapular angles short and visible in dorsal view. Humeral angles with a pair of pointed teeth. Pronotal sides straight. Pronotal carina marked, superficially crenulate on the sides only, and interrupted on the middle by a superficial depression. Mesonotum and scutellum flat in side view. Lower mesopleurae with traces of a small denticle. Basal face of the propodeum short. Sides of the basal face of the propodeum with two pairs of teeth, the anterior pair round and small, the posterior pair more pointed. Sides of the declivous face of the propodeum converging posteriorly.

Petiole with deeply concave anterior face and anteriorly declivous dorsally; anterior half of the petiolar sides diverging into a pair of pointed teeth, the posterior half converging posteriorly. Postpetiole broadly convex dorsally; sides of the postpetiole with a pair of broad spines arising from the anterior border and curved backwards.

Gaster weakly protruding anteriorly and with the margination not reaching the first stigma posteriorly.

Legs. Fore coxae angulate. Hind femora angulate. Mid and hind basitarsi compressed laterally, their proximal part broader than the distal one.

Sculpture. Dorsum of the head, of the pronotum, of the mesonotum and of the scutellum minutely punctate and with variably clumped foveae, diminishing in size on the anterior half of the head, shallower on the frontal carinae, larger on the pronotum. Ventral part of the head with sculpture similar to the one on the pronotum but with the foveae deeper on the sides. Basal face of the propodeum, pedicel and upper mesopleurae with irregular, dense, foveae. Propleurae reticulate and with foveae anteriorly and superiorly only; propleurae with additional longitudinal, thin rugosities on the posterior third. Lower mesopleurae reticulate and with foveae on the borders only; their centre with thin, faint, longitudinal rugosities. Metapleurae reticulate and with longitudinal rugosities. Outer face of the fore and hind coxae with short, transversal, thin, rugosities. Outer face of the mid coxae with longitudinal, thin rugosities. Gaster and legs reticulate. Anterior third of the first gastral tergite with irregular, superficial foveae; outer face of the distal part of the femora and the outer face of the tibiae with sculpture similar to the one of the first gastral tergite but with smaller foveae.

Pilosity. As in the other species of the clade.

Colour. Black with lighter legs. Frontal carinae opaque, dark ferruginous to brown.

Measurements (in mm) and indices: TL 10.22; HL 1.88; HW 2.12; EL 0.50; PW 2.08; PeW 0.98; PpW 1.12; HBaL 0.62; HBaW 0.24; CI 112.8; PI 101.9; PPeI 212.2; PPpI 185.78; HBaI 38.7.

Material examined. - **Brazil**: Piauí: Canto do Buriti, 18–27.XI.1991, 8 workers, C. R. F. Brandão [MZSP]; 10 km N of Corrente, Fazenda Maracujá, 23–27.XI.1991, 5 workers, C. R. F. Brandão [MZSP]. Goiás: Jataí, XII.1972, 2 workers, F. M. Oliveira [MZSP]; Jataí, Fazenda Cachoeirinha, 29.XI.1962, 1 gyne, Exp. Dept. Zool. [MZSP]; 70 km NW of Alto Paraíso, Morro das Cobras, 01–0 7.VII.1991, 4 workers, C. R. F. Brandão, M. L. Françoso & A. A. Reis [MZSP]. Bahia: Santa Rita de Cassia, Riacho Veredão, 13–18.VII.1991, 1 worker, C. R. F. Brandão [MZSP]. Distrito Federal: Reserva Biológica de Águas Emendadas, 27–30.VI.1991, 1 worker (holotype), 182 workers (paratypes), 12 soldiers (paratypes), C. R. F. Brandão, M. L. Fraçoso & A. A. Reis [MZSP]; E. Ecol. Águas Emendadas, 25.I, 31.III, 25.V, 19.VII, 30.IX, and 23.XI.1992, 239 workers, 41 soldiers, A. Reis [MZSP]. Mato Grosso: Chapada dos Guimarães, Véu de Noiva, 21.XII.1984, 1 worker, 8 soldiers, J. C. Trager [MZSP]. Mato Grosso do Sul: Xavantina, Rio das Mortes, 1 worker, M. Alvarenga [MZSP]. São Paulo: Mogi Guaçu, Fazenda Campininha, XI.1977, 3 workers, H. C. M. [MZSP].

Discussion. - The worker of *betoi* is very similar to that of *pavonii*. The similarity between the two species induced Kempf (1972) to recognise a unique, broadly distributed, *pavonii*. The examination of additional material collected after the death of Kempf (including workers associated with soldiers) permitted the first separation of the two species.

The longitudinal rugosities on the pleurae and on the declivous face of the propodeum in both neuter castes and the other characters mentioned under the

diagnosis allow a clear distinction of *betoi* from all the other species of the *depressus* clade regardless of the amount of material available.

Distribution: Brazil.

Cephalotes depressus (KLUG) new combination
Figs. 155, 156, 157, 388 (bottom)

Cryptocerus depressus KLUG, 1824: 204. Worker. Original description. Type locality: Guanabara, Rio de Janeiro. Type material: not available for the present study.

Cryptocerus depressus KLUG, EMERY, 1905: 170. Soldier.

Cryptocerus depressus KLUG, FOREL, 1906: 235. Gyne. Nec male (= *eduarduli*).

Cryptocerus depressus var. *sorocabensis* FOREL, 1912: 200. Soldier. Original description. Type locality: Sorocaba (São Paulo). Type material 7 workers and 2 small soldiers labelled: "Sorocaba, Prov. St. Paolo, Göldi, *C. depressus* v. *sorocabensis* For., type", examined. Synonymy by KEMPF, 1951: 218.

Paracryptocerus depressus (KLUG), KEMPF, 1951: 218, figs. 141, 148. Worker, soldier, gyne. First combination in *Paracryptocerus*.

Zacryptocerus depressus (KLUG), OLIVEIRA & SAZIMA, 1984: 145. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *depressus* clade differing from its sister species *eduarduli*, in the worker, soldier and gyne by the absence of erect, truncate hairs on the mesosoma, on the pedicel and on the first gastral tergite, in the soldier and in the gyne by the head dorsum opaque.

Worker (Fig. 155) (description of KEMPF, 1951). - "Length 4.5–6 mm. Black; the following ferruginous to testaceous: frontal carinae, occipital lobes, tips of lateral spines on thorax and peduncle, and anterolateral border of gaster. Reddish-brown to fuscous-brown: Mandibles, antennae, tibiae, and tarsi.

Head subquadrate, slightly broader than long. Frontal carinae distinctly crenulate and beset with small projecting setulae on the anterior half; very little diverging caudad. Occipital lobes bidenticulate, the inner tooth subacute, the outer tooth blunt. Pronotal lamellae short, not longer than broad, the second tooth of the pronotum, behind the lamella small, smaller than the lateral mesonotal tooth. First lateral epinotal spine not recurved, the second spine very short, in the form of a triangular tooth, removed from the posterior corner of the declivous face. Petiole with a lateral slender spine, arising from the side, its base removed backward from the often subangulate anterior corner of the segment. Postpetiole with an anterior lateral stout spine, recurved at apex. Gaster subcordiform, longer than wide, longer than the interocular width. The anterolateral border of the first tergite distinctly but narrowly crested."

Measurements (in mm) and indices: TL 4.20–580; HL 0.92–1.32; HW 1.16–1.72; EL 0.32–0.44; PW 1.00–1.68; PeW 0.64–0.98; PpW 0.55–0.76; HBaL 0.32–0.48; HBaW 0.10–0.19; CI 126.1–130.3; PI 103.1–116.0; PPeI 156.2–171.4; PPpI 181.8–221.0; HBaI 31.2–39.6.

Soldier (Figs. 156, 388 bottom) (description of KEMPF, 1951). - "7 mm. Black; the following lighter, more or less ferrugenous: anterior portion of frontal carinae, tips of femora, tibiae and tarsi, tips of lateral pronotal and epinotal lobes, peduncular spines.

Head subquadrate, the upper surface of head rather convex. Frontal carinae sharply crenulated, with small setulae projecting from the notches. Vertex with a vestigial transverse median carinule, the small teeth more or less vestigial; occiput subtruncate. Upper surface of head finely punctate and subfulgid. Shoulders distinct, pronotum greatly expanded laterad, the posterior portion, of the sides strongly converging and somewhat emarginate. Transverse pronotal crest vestigial mesad. Mesonotum with a rounded lateral lobe. Basal face of epinotum very short mesad, with a postero-lateral bituberculate on each side, the base of which forms a faint carinule separating the declivous face from the basal face, fading out towards the middle. Petiole and postpetiole as in worker, the petiole still narrower, the lateral spines shorter. The postpetiole with stouter, more recurved lateral spines."

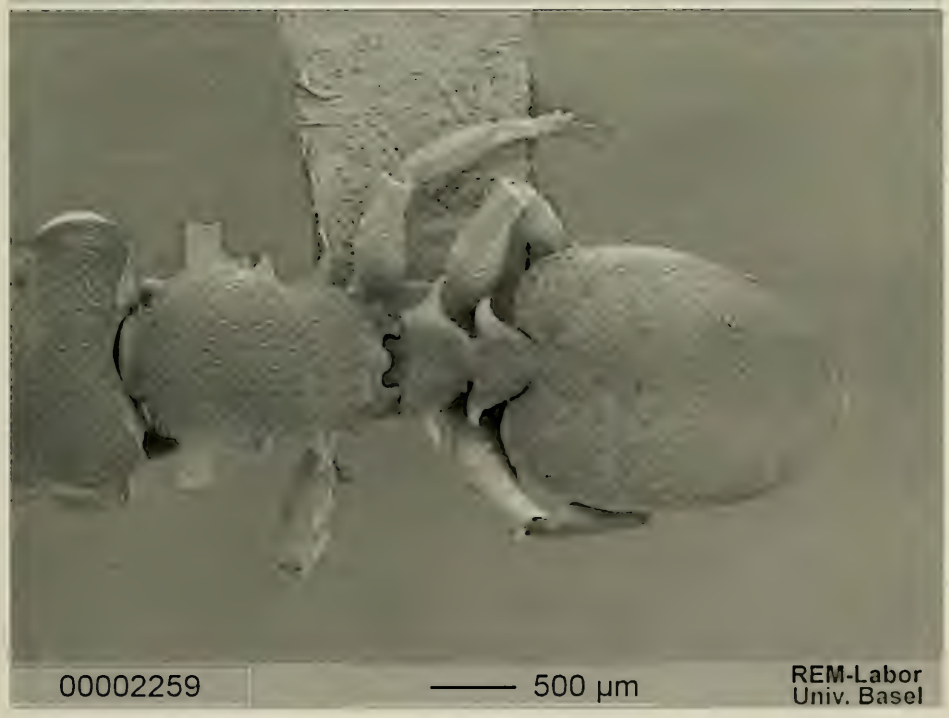


Fig. 155. *Cephalotes depressus* (KLUG). Worker from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 156. *Cephalotes depressus* (KLUG). Soldier from Chapada dos Guimarães (Mato Grosso), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 6.44–7.08; HL 1.60–1.76; HW 2.00–2.22; EL 0.44; PW 1.96–2.12; PeW 0.96–1.08; PpW 0.84–0.94; HBaL 0.52–0.56; HBaW 0.20; CI 124.4–126.1; PI 102.0–104.7; PPeI 196.30–204.1; PPpI 225.5–238.1; HBaI 35.7–38.5.

G y n e (description of KEMPF, 1951). - "Length 10 mm. In general similar to that of *cristatus*. Frontal carinae regularly and very sharply crenulate. Vertex without a distinct median bicarinate crest. Occipital angle simple, not bidenticulate. Transverse pronotal crest not serrated, with a more or less continuous edge. Scapular spine short, directed sideward, not foreward. Lower mesopleura without a conspicuously projecting tooth, usually more or less obsolete. Epinotal teeth shorter. Petiole about as long as wide, sides sub-parallel, constricted behind, the sides forming a small, rectangular denticle in front of the constriction. Postpetiole somewhat broader than long, much narrower than in *cristatus*. Wings infuscated, the veins dark brunneous. Fore wing with a closed and appendiculate marginal cell, the transverse cubital vein present."

Measurements (in mm) and indices: TL 9.52–10.16 HL 1.80–1.84; HW 2.04–2.08; EL 0.48; PW 1.92–2.08; PeW 0.80–0.92; PpW 1.00–1.06; HBaL 0.68–0.70; HBaW 0.24–0.25; CI 113.0–113.3; PI 100.0–106.2 PPeI 226.1–240.0; PPpI 1.92.0–196.2; HBaI 35.3–35.7.

M a l e (previously undescribed). - Head (eyes included, mandibles excluded) 1/3 broader than long; vertexal angles obtuse and carinate. Ocelli protuberant on the convex vertex. Eyes broadly convex and placed in the middle of the sides of the head. Frontal carinae raised, diverging backwards and not reaching the posterior border of the eyes. Frons flat. Clypeus convex dorsally. Mandibles slender, laterally carinate and with three distinct apical teeth. Scapes thick, twice longer than the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view broadening backwards; its sides with a superficial lateral carina in some specimens only. Mesonotum convex; median Mayrian carina and parapsidal furrows weakly impressed. Scutellum convex, its sides converging posteriorly. Propodeum with slightly differentiate basal and declivous faces; basal face convex, its sides converging posteriorly.

Petiole narrower than postpetiole with a deeply concave anterior border. Sides of the petiolar node convex and posteriorly converging. Postpetiole convex in dorsal view; its sides anteriorly with an obtuse, short denticle or gently convex.

Gaster as broad as or broader than the mesosoma.

Genitalia and subgenital plate as in Fig. 157.

Wings. Fore wings with *R+Sc* superficially connected with a marked pterostigma. *2r* marked, *Rsf5* connected with *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; *CuA*, *M* and distal part of *1A* vestigial.

Sculpture. Body covered by deep reticulation less impressed on the gaster and on the legs. Head dorsum with small, superficial foveae, denser on the posterior fourth and on the frons. Periocular area with transversal rugosities. Ventral part of the head and mesosoma with large, deep, irregular foveae. Pleurae with longitudinal, thin rugosities; mesopleurae with very superficial, small foveae. Pedicel with few rugosities.

Pilosity. Head and mesosoma covered by long, dense, suberect, hairs, sparser and subdecumbent on pedicel, on the gaster and on the legs. Funiculi densely covered by thin, short, decumbent hairs, similar but thinner, sparser and slightly longer hairs on the legs and on the gaster.

Colour. Head, mesosoma and pedicel black; proximal half of the legs and gaster light brown to black. Distal half of the legs and wing veins yellowish brown. Wings slightly infuscated and transparent.

Measurements (in mm) and indices: TL 5.40–6.38; HL 0.80–0.90; HW 1.12–1.24; EL 0.39–0.46; PW 0.96–1.12; PeW 0.48–0.64; PpW 0.56–0.70; HBaL 0.50–0.60; HBaW 0.11–0.13; CI 135.6–140.0; PI 108.9–116.7 PPeI 192.3–200.0; PPpI 166.7–171.4; HBaI 20.3–23.5.

M a t e r i a l e x a m i n e d . - **Venezuela**: P. Anduze, Surukum, III.1942, 1 worker [MCZC].

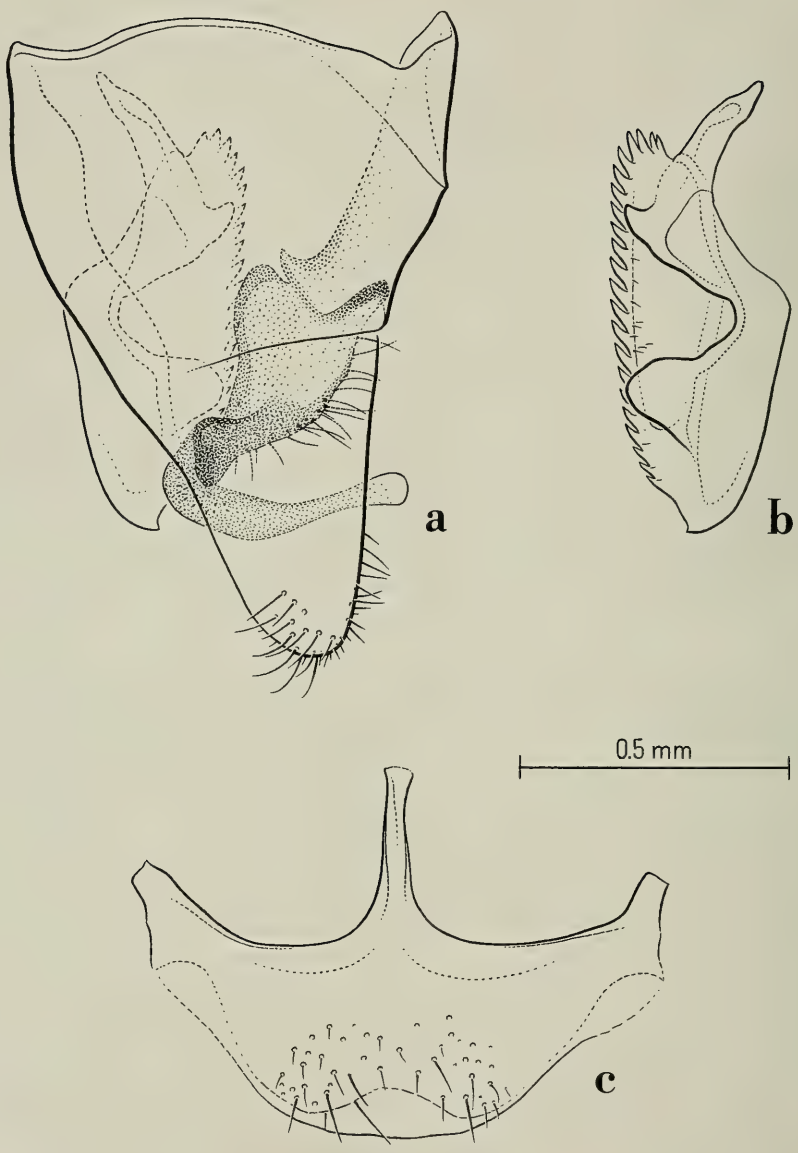


Fig. 157. *Cephalotes depressus* (Klug). Male from Agudos (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Guyana: Georgetown, III.1955, 1 worker, M. ALVARENGA [MZSP].

Ecuador: Prov. Napo, 00°24' S, 76°36' W, Limoncocha, 16.VII.1972, 2 workers, 1 gyne, C. RETTENMEYER [MZSP].

Brazil: no further locality, 2 gynes [MNHN, MCSN]. A m a p á : Macapá, 5.V.1979, 1 worker, W. L. OVERAL [MPEG]. A m a z o n a s : Manaus, 4 workers, 1 gyne, 1 male, MANN & BAKER [MCZC]; same locality, 5 workers, 1 soldier, W. M. MANN [MZSP]; same locality, ORIS, Entr. Mauá, km 3, 15.IX.1977, 1 worker, C. GONDIN [INPA]; km 60 INPA, 1 worker, III.1986, G. COUTURIER [CPCC]. P a r á : no further locality, 20.VI.1974, 1 worker [CPCC]; Santarém, Taperinha, 2° 54' S 54° 20' W, VII. 1975, 5 workers, R. L. JEANNE [MCZC, MZSP]; Cachimbo, VI.1962, 1 worker, M. ALVARENGA & F. M. OLIVEIRA [MZSP]; Alto Cuminá, 27.XII.1928, 2 workers, SAMPAIO [MZSP]; Rio Cuminá, 1928, 1 worker, 2 soldiers, SAMPAIO [MZSP]; Monte Alegre, 26.I.1949, 2 workers, C. R. GONÇALVES [MZSP]; Conceição do Araguaia, 24.I.1983, 1 worker, A. Y. HARADA [MZSP]; same locality, Redenção, 25.XI.1978, 17–21.XI.1979, 1 worker, 1 gyne, R. B. NETO [MPEG]. P e r n a m b u c o : Tapera, 1 worker, 1 soldier, B. PICKAL [MZSP]. R o n d ô n i a : Vilhena, XI.1973, 1 worker, M. ALVARENGA [MZSP]; same locality, 25.VII.1983, Polo Noroeste, capoeira, vegetação trepadeira, 1 worker, A. Y. HARADA [INPA]. D i s t r i t o F e d e r a l : Estação Ecológica Águas Emendadas, 31.III.1992, 3 workers, A. Reis [MZSP]; Reserva Biológica de Águas Emendadas, 30.VI.1991, 2 workers, C. R. F. BRANDÃO, L. FRANÇOSO & A. A. REIS [MZSP]. G o i á s : Jataí, XI.1971, 4 workers, F. M. OLIVEIRA [MZSP]; Campinas, 1 worker, 1 soldier [MZSP]; Parque Nacional das Emas, 24.IX.1994, 6 workers, 6 soldiers, C. R. F. BRANDÃO [MZSP]. B a h i a : Vitória da Conquista, 27.I.1994, 1 worker, 1 soldier, 1 gyne, 1 male, J. H. C. DELABIE [CPCC]; Encruzilhada, 960 m, XI.1972, 1 worker, SEABRA & ALVARENGA [MZSP]; Mucugê, Meio Montanha, 6–12.XII.1990, 2 workers, C. R. F. BRANDÃO, J. M. DINIZ & P. S. OLIVEIRA [MZSP]. M a t o G r o s s o : Utiariti, Rio Papagaio, 24.X.1966, 4 workers, LENKO & PEREIRA [MZSP]; Utiariti, Rio Papagaio, 325m, VIII.1961, 3 workers, K. LENKO [MZSP]; Poconé, 22.IV.1972, 13 workers, 1 soldier, 2 gynes, R. N. WILLIAMS [MZSP]; Chapada, V.1959, 2 workers, Fr. CANUTO [MZSP]; Chapada dos Guimarães, Ponto mirante, 08.XI.1984, 15 workers, 8 soldiers, J. C. TRAGER [MZSP]; Chapada dos Guimarães, Fazenda Buriti, 09–14.II.1966, 1 worker, C. R. F. BRANDÃO & F. CAETANO [MZSP]; U. H. Manso, Campo cerrado grotão, 16.VIII.1988, 1 worker, H. C. MORAIS [MZSP]. M a t o G r o s s o d o S u l : 3 km from Ponta Porã, 15.X.1989, 3 workers, B. H. DIETZ [SMNS]; Corumbá, Fazenda Sta. Blanca, 08.XII.1960, 1 worker, K. LENKO [MZSP]; Corumbá, Porto Esperança, 7.XII.1960 1 worker, K. LENKO [MZSP]; Nioaque, 25.VII.1971, 1 worker, R. TRAVASSOS [MZSP]; Três Lagoas, Fazenda Canaã, 4.V.1962, 12 workers, 7 soldiers, 1 gyne, F. LANE [MZSP]; Três Lagoas, Fazenda Yamaguti, Córrego da Onça, IX.1964, 1 worker, Exp. Dep. Zool. [MZSP]; Três Lagoas, Fazenda Canaã, left side of the Rio Sucurú, IV.1967, 1 worker, F. LANE [MZSP]; Três Lagoas, Fazenda Retiro de Telhas, 22.V.1964, 20 workers, 14 soldiers, 3 gynes [MZSP]; Três Lagoas, Fazenda Retiro de Telhas, 16.X.1964, 14 workers, 3 soldiers, Exp. Dep. Zool. [MZSP]; Campo Grande, 9.X.1961, 7 workers, F. M. OLIVEIRA [MZSP]; Jardim, I.1962, 1 worker, R. MUELLER [MZSP]; Paranaíba, Fazenda Fortaleza, 19.II.1970, 3 soldiers, J. M. DINIZ [MZSP]. M i n a s G e r a i s : Pedra Azul, I.1971, 1 worker, 1 soldier, 1male, F. M. OLIVEIRA [MZSP]; Lavras, 7.XII.1978, 1 worker, W. D. FRANK [MCZC]; Pedra Azul, 800m, XI.1972, 6 workers, 1 soldier, SEABRA & ALVARENGA [MZSP]; Passa Quatro, XII.1972, 1 gyne, F. M. OLIVEIRA [MZSP]. S ã o P a u l o : Agudos, 31.III.1952, 12 workers, W. W. KEMPF [MZSP]; same locality and collector, 23.V.1952, 5 workers, 1 soldier, 1 male [MCZC]; same locality and collector 07.IX.1952, 4 workers, 2 gynes, 2 males, [MCZC]; Avaré, 14.IX.1974, 4 workers [MZSP]; same locality, 15.XI.1971, 2 workers, F. LANE [MZSP]; Avaré, Fazenda Guarujá, 22.IV.1972, 6 workers, F. LANE [MZSP]; Barueri, 27.I.1962, 1 worker, K. LENKO [MZSP]; Botucatu, 12.IV.1964, 1 worker, L. LANE [MZSP]; Botucatu, 29.I.1996, 2 workers, M. L. DE ANDRADE [SMNS]; Botucatu, Três Pedras, 7.VII.1944, 7 workers, 5 soldiers, 4 gynes, B. H. DIETZ [MZSP]; Campinas, 14.XII.1973, 2 workers, L. LANE [MZSP]; Campo Limpo, X.1966, 2 workers, L. KRELESBACH [MZSP]; Embú, 09.XI.1974 2 workers, L. LANE [MZSP]; Franca, II.1911, 13 workers, 3 soldiers, 2 males, E. GARBE [MZSP]; Itú, 09.X.1960, 15 workers, WERNER-MARTINS [MZSP]; Mogi Guaçu, Fazenda Campininha, 17.IX.1977, 4 workers, 1 soldier, 1 gyne, 1 male, H. C. M. [MZSP]; Nova Europa, Fazenda Itaquerê, 24.VIII.1963, 3 workers

[MZSP]; Pindamonhangaba, II.1949, 1 gyne, SCHWARZMEIER [MZSP]; Piracicaba, sitio Cedro Velho, 03.XII.1989, 1 worker, C. R. F. BRANDÃO [MZSP]; São Carlos, 17.III.1990, 1 worker, M. L. DE ANDRADE [SMNS]; Jundiaí, 05.XII.1961, 1 worker, WERNER [MZSP]; São Paulo, 1 worker, JHERING [MHNG]; Sorocaba, 7 workers, 2 soldiers, GÖLDI [MHNG]; São Paulo, 11 workers, 4 soldiers, REH [MHNG]; Ipiranga, 20.X.1906, 2 workers, 1 gyne [MZSP]; Tietê, 18.I.1990, 1 gyne, M. L. DE ANDRADE [ZSMC]. Rio de Janeiro: Represa Rio Grande, IV.1966, 1 worker, M. ALVARENGA [MZSP]. Santa Catarina: Nova Teutônia, 27°11' B, 52°23' L, 300–500 m, several collecting dates, 43 workers, 5 soldiers, 10 gynes, 4 males, F. PLAUMANN [MCZC, MZSP]. Rio Grande do Sul: S. Augusto, XII.1975, 6 workers, B. ROPPA [MZSP]; Mato Leitão, 30.XI.1996, 22 workers, 4 soldiers, E. SONHUDO [MZSP].

Bolivia: Beni: Rosario, Rogagua Lake, 1921–1922, 1 worker, 1 gyne, 1 male, W. M. MANN, [MZSP].

Argentina: Chaco: Colonia Benitez, 07.XII.1948, 1 worker, GOLBACH [MZSP]; Misiones: Est. Exp. Loreto, 1932, 2 workers, 1 gyne, 1 male, A. A. OGLOBIN [NHMB, MZSP]; Loreto Alem. 1958, 10 workers, 1 male, N. KUSNEZOV [MZSP]; San Ignacio, 5 workers, C. BRUCH [NHMB]; Env. de San Ignacio, Villa Lutécia, 1910, 1 gyne, E. R. WAGNER [NHMB]. Corrientes: Bompland, 1 worker, JÖRGENSEN [NHMB]; San Roque, 3 workers, J. BOSQ. [NHMB].

Paraguay: no further locality, 2 workers, 1 gyne, BALZAN [MCSN]. Presidente Hayes: Asunción, VII.1961, 1 worker, N. L. H. KRAUSS [USNM]; Aregua, 20 mi E of Assunción, 16.VIII.1980, 1 male, D. C. LOWRIES [USNM]. La Cordillera: San Bernardino, 1 gyne, K. FIEBRIG [USNM]. Alto Paraná: Pastoreo, IX-XII.1974, 5 workers, P. DUELLI [MZSP]; San Bernardino, 1 worker [NHMB]; San Bernardino, 27 April, 39 workers, 3 soldiers, 5 gynes, K. FIEBRIG [ZSMC, MCZC, MHNG]; Sa. Trinidad, IX.1913, 1 gyne, ZÜRCHER [NHMB].

Discussion. - Three specimens from Ecuador (two workers and a gyne on a separate pin) differ from other *depressus* specimens for having much lighter and sparser body sculpture and thinner hairs. On the base of the material available for the present study we consider these specimens as representing an extreme of geographical variation within *depressus*. A worker from São Carlos and some of the syntypes of the variety *sorocabensis* have the second pair of propodeal spines reduced or absent.

A gyne from Paraguay collected by Balzan (MCSN) does not differ significantly from other gynes of *depressus* except for its dwarf size (total length 8.08 mm instead of > 9.5 mm).

Distribution: Venezuela, Guyana, Ecuador, Brazil, Bolivia, Argentina, Paraguay.

Cephalotes eduarduli (FOREL)
Figs. 158, 159, 160, 161, 162, 163

Cryptocerus depressus KLUG, FOREL, 1906: 235. Male. Nec worker, soldier and gyne. Misidentification.

Cryptocerus eduarduli FOREL, 1920: 204. Worker, soldier and gyne. Original description. Type locality: Concepción, Paraguay. Type material 26 workers, 18 soldiers, 10 gynes, all syntypes, labelled "Concepcion, Paraguay, in *Agonandra brasiliensis*, Chodat", in MHNG, examined.

Cryptocerus pavonii (LATREILLE), EMERY, 1890: 73, pl. 8, figs. 8–9 (nec LATREILLE, 1809). Soldier. Nec worker and gyne. Vide *borgmeieri*. Misidentification.

Paracryptocerus eduarduli (FOREL), KEMPF, 1951: 221. First combination in *Paracryptocerus*.

Paracryptocerus eduarduli (FOREL), KEMPF, 1958: 15, fig. 25. Soldier.

Zacryptocerus eduarduli (FOREL), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Cephalotes eduarduli (FOREL), BARONI URBANI, 1998: 326, fig. 7. Soldier and gyne. First combination in *Cephalotes*.

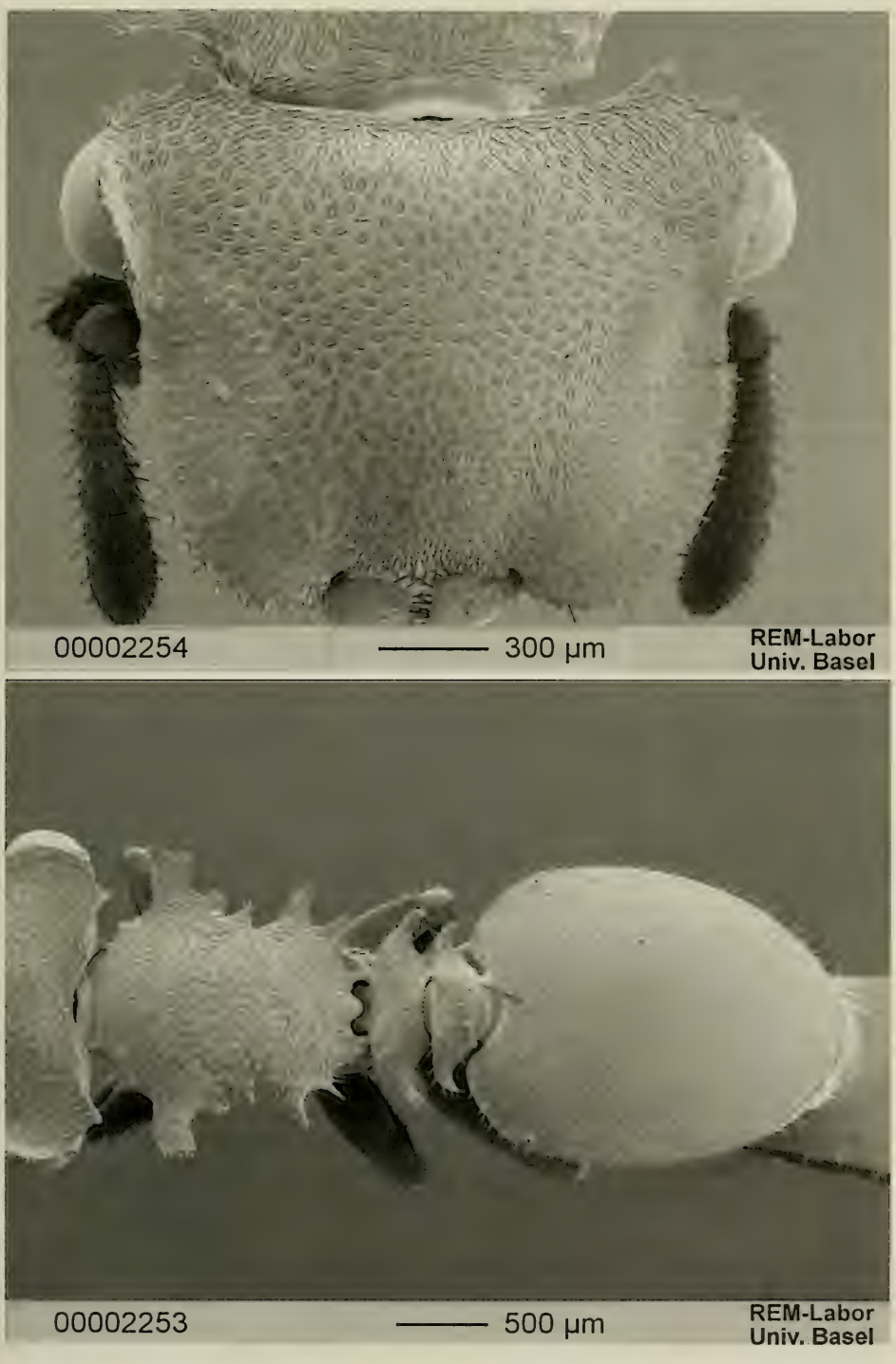


Fig. 158. *Cephalotes eduarduli* (FOREL). Worker from Várzea Grande (Mato Grosso), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

D i a g n o s i s . - A member of the *depressus* clade differing from its sister species *eduarduli*, in the worker, soldier and gyne, by the erect, truncate hairs on the mesosoma, on the pedicel and on the gaster, in the worker only by short pronotal lamellae and, in the soldier and in the gyne, by the shining head.

W o r k e r (Fig. 158). - Head subquadrate. Vertexal angles with two pairs of teeth, the external pair small, sometimes denticulate, obtuse, the internal one large, triangular and lamellaceous. Vertexal border deeply concave. Genae completely marginate below. Frontal carinae crenulate, broad, strongly upturned over the eyes and extending up to their posterior border backwards. Clypeal border incised. Mandibles with superficial lateral carinae. Eyes strongly convex.

Mesosoma convex in side view. Scapular angles well visible in dorsal view. Pronotal sides with a pair of lamellae followed by a deep notch and a pair of variably pointed or round teeth; pronotal lamellae narrow, rectangular, directed laterally and with bidentate or crenulate border. Mesonotum with a pair of pointed teeth. Promesonotal suture superficial in some specimens. Propodeal suture dorsally obsolete and variably impressed on the sides only. Propodeum sloping backwards, without differentiate basal and declivous faces; its sides with two pairs of pointed spines, the anterior pair broad and gently recurved in some specimens, the posterior one thinner and smaller than the first pair. Petiole almost flat and slightly broader than the postpetiole, its dorsum sloping anteriorly. Petiolar spines making an obtuse angle with the anterior border of the petiole, curved backwards, with truncate and crenulate apex. Postpetiolar spines curved with the apex pointing backwards.

Gaster with a thin, narrow margin not surpassing the stigma posteriorly.

Hind and mid femora with a pair of median denticles; mid and hind basitarsi laterally compressed and with the proximal part broader than the distal one.

Sculpture. Head dorsum superficially and minutely reticulate and with small foveae as broad as or slightly broader than their interspaces, larger and denser posteriorly, superficial on the frontal carinae. Ventral face of the head reticulate, with sparse, shallow foveae and with superimposed, short rugosities under the eyes. Pronotum and mesonotum reticulate and with foveae as broad as on the posterior part of the head, dense on the pronotum, sparser on the mesonotum. Anterior half of the propodeum and peduncular segments reticulate and with superficial, oval foveae. Posterior third of the propodeum with thin, longitudinal rugulae. Sides of the mesosoma reticulate, with oval foveae on the anterior part of the propleurae and on the posterior part of the meso- and metapleurae, this sculpture superimposed by thin, longitudinal rugosities. Tergites, distal part of the outer face of the femora and outer face of the tibiae strongly reticulate and with superficial, small foveae. Middle of the first gastral sternite and sides of the femora superficially shining.

Pilosity. Each fovea bearing an appressed hair of size proportional to the one of the foveae. Parts of the gaster and of the legs without foveae with thin hairs. Notches of the frontal carinae, mandibles, trunk, peduncular segments, gaster and legs with suberect, truncate hairs, denser on the apex of the gaster. Rare, suberect, long, pointed hairs on the apex of the sternites.

Colour. Black. Frontal carinae, border of the pronotal lamellae, apices of the thoracic and peduncular spines, extensor faces of the tibiae and tarsomeres orange-ferruginous.

Measurements (in mm) and indices: TL 4.76–5.64; HL 1.08–1.28; HW 1.44–1.68; EL 0.36–0.44; PW 1.48–1.72; PeW 0.97–1.12; PpW 0.80–0.96; HBaL 0.44–0.57; HBaW 0.15–0.20; CI 131.0–133.3; PI 97.3–100.0; PPeI 152.5–158.3; PPpI 1.72.1–190.0; HBaI 31.2- 35.1.

S o l d i e r (Fig. 159) (description of Kempf, 1958). - „Total length 7.8 mm. Maximum length of head 2.39 mm; of thorax 2.25 mm. Black; funiculus and apical four tarsites of all legs fuscous-brown.

Head wider than long (75:67). Mandibles finely punctate, opaque, their outer border distinctly angulate at the middle. Frontal carinae with scarcely crenulate border. Dorsum of head rather convex discad, sparsely foveolate, very finely punctate, shiny. Sides of head emarginate above the flattened eyes. Occipital angles obliquely truncate, marginate, the

margination forming an obtuse tooth on each end. Vertex with a pair of projecting teeth in the middle, which are connected by a vestigial transverse carinule. Occiput perpendicular to vertex, its posterior border slightly convex. Gular face of head more coarsely reticulate-punctate, with rather oblong foveolae.

Thorax wider than long (73:63), subopaque, more coarsely punctate. Sides longitudinally rugose, the rugosities forming meshes on the mesopleura. Shoulders indistinct. Pronotum greatly expanded laterad, with an elevated, straight-edged, transverse crest, which is broadly interrupted mesally, and has laterally one or two shallow notches. Anterior corner of pronotal expansions with a pointed tooth. Behind the transverse crest, the sides of the pronotum are sinuous and converge strongly mesad. Promesonotal suture distinct. Sides of mesonotum with a large, rounded and projecting lobe. Mesoepinotal suture deeply impressed. Basal face of epinotum having on its posterior corner a stout lobe, which projects outward and upward, and bears on its apex two bluntly rounded teeth, the posteriormost tooth being largest and almost erect. Declivity not separated from the basal face by a carinule. Hind femora angulate and denticulate above, in the distal half.

Peduncular segments thrice as broad as long. Sculpture as on thorax, the foveolae being somewhat elongate. Petiole broader than postpetiole, bearing on each side a strong, acute, spine, which curves obliquely caudad. Postpetiole with a similar spine on each side, the apex of which points directly caudad.

Gaster longer than broad (70:60). Anterior border shallowly emarginate in the middle. First tergite opaque, finely and densely punctured, with scattered, more conspicuous piligerous points. Sternites and apical border of tergites with standing hair."

Measurements (in mm) and indices: TL 6.80–8.16; HL 1.68–2.08; HW 2.12–2.56; EL 0.48–0.53; PW 2.08–2.68; PeW 1.20–1.32; PpW 1.00–1.22; HBaL 0.58–0.63; HBaW 0.21–0.23; CI 121.1–126.5; PI 95.5–101.9; PPeI 173.3–216.1; PPpI 208.0–233.3; HBaI 36.2–37.7.

G y n e (Fig. 160). - Head convex, without disc. Frontal carinae broad and with crenulate border; sides of the frontal carinae converging in front of the eyes and reaching the middle of the eyes. Vertexal angles with two pairs of small, obtuse denticles. Vertex with a pair of median, small denticles or protuberances. Clypeus slightly concave or incised anteriorly. Mandibles broad, with a lateral, carinate tumulus.

Mesosoma. Humeral angles with a pair of pointed anterior teeth. Pronotal sides straight. Pronotal carina narrow, not crenulate and superficially interrupted in the middle. Mesonotum and scutellum flat.

Lower mesopleurae with a small denticle. Basal face of propodeum generally with two pairs of teeth, the anterior pair sometimes absent or smaller and less pointed than the posterior ones; declivous face flat.

Petiole with the anterior border concave, its dorsum sloping anteriorly; petiolar sides with a pair of small, pointed spines. Postpetiole convex dorsally; sides of the postpetiole with a small, broad, obtuse tooth in their cranial half.

Gaster with a broad, not cranially protruding anterior border.

Legs. Fore coxae with a broad lobe anteriorly. Hind femora medially angulate. Hind basitarsi flat and broadened at their base.

Wings (Fig. 161). Fore wings with *R+Sc* superficially connected to a marked pterostigma. *2r* marked, *Rsf5* connected with *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; distal part of *M*, of *CuA* and of *1A* vestigial.

Sculpture. Head minutely and superficially punctate and covered by small foveae as broad as their interspaces, larger and deeper on the posterior part, superficial on the frontal carinae. Ventral part of the head reticulate and opaque anteriorly, shining posteriorly, the reticulation superimposed by deep foveae, slightly larger than those on the posterior part of the head dorsum. Mesosoma and pedicel reticulate-punctate and with foveae larger than those on the head dorsum, the foveae denser on the posterior part of the pronotum, on the basal face of the propodeum, on the petiolar sides, on the postpetiole, on the two posterior thirds of the mesopleurae and on the middle of the metapleurae. Pleurae with superficial, thin, longitudinal rugosities. Declivous face of the propodeum reticulate only. First gastral tergite and sternite

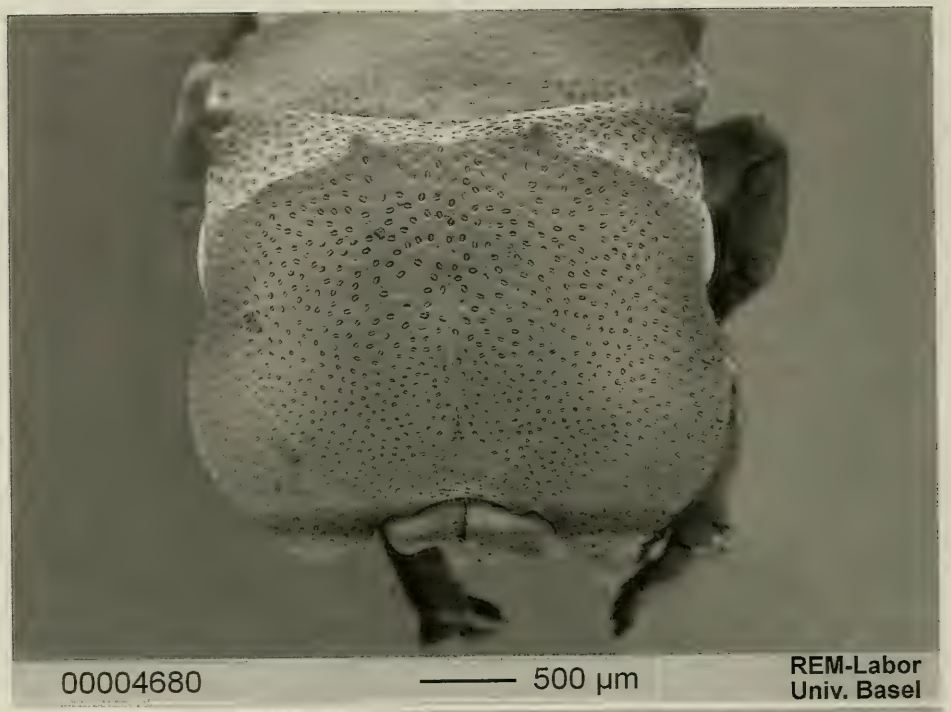


Fig. 159. *Cephalotes eduarduli* (FOREL). Soldier from Várzea Grande (Mato Grosso), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

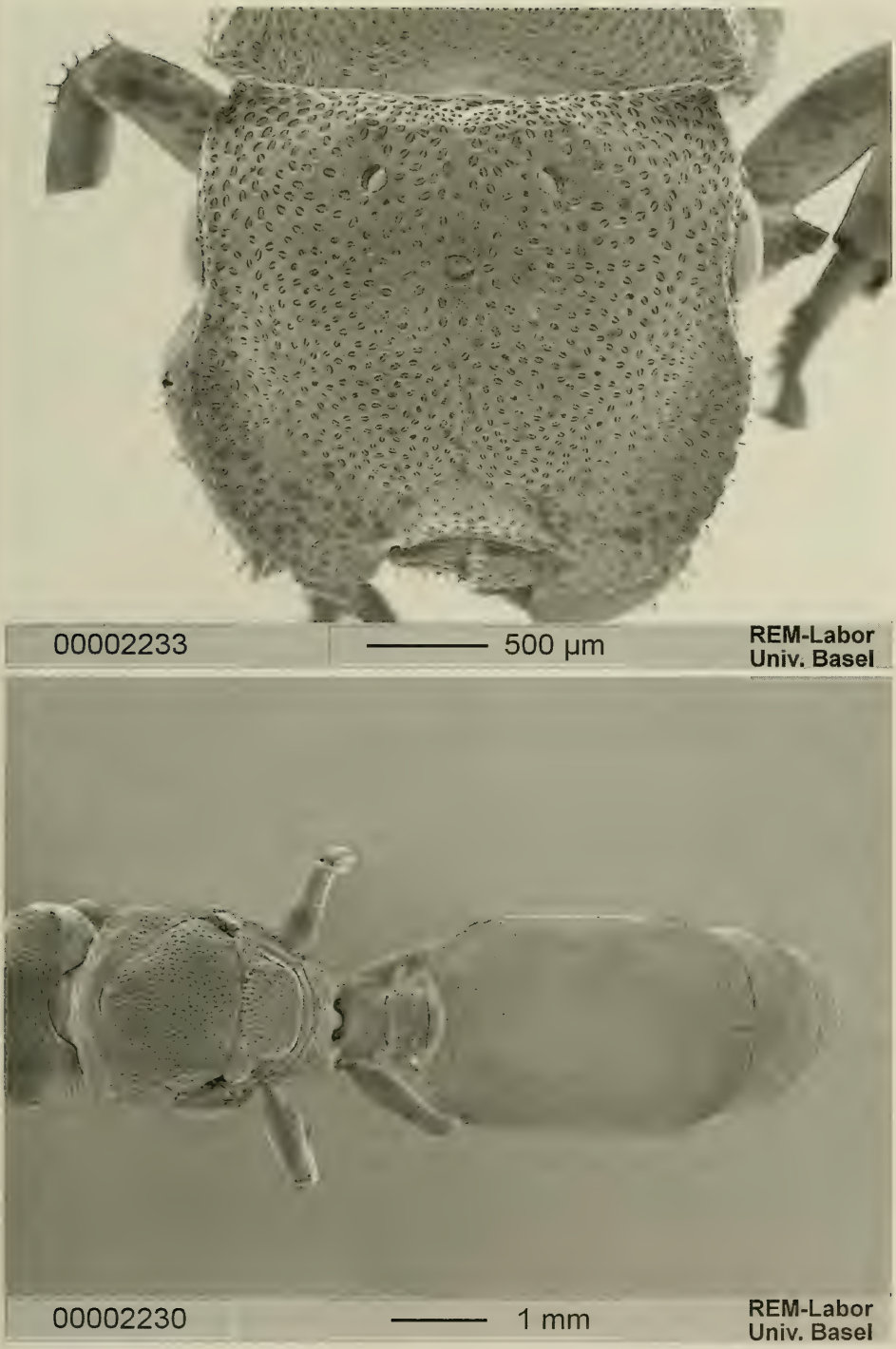


Fig. 160. *Cephalotes eduarduli* (FOREL). Gyne from Várzea Grande (Mato Grosso), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

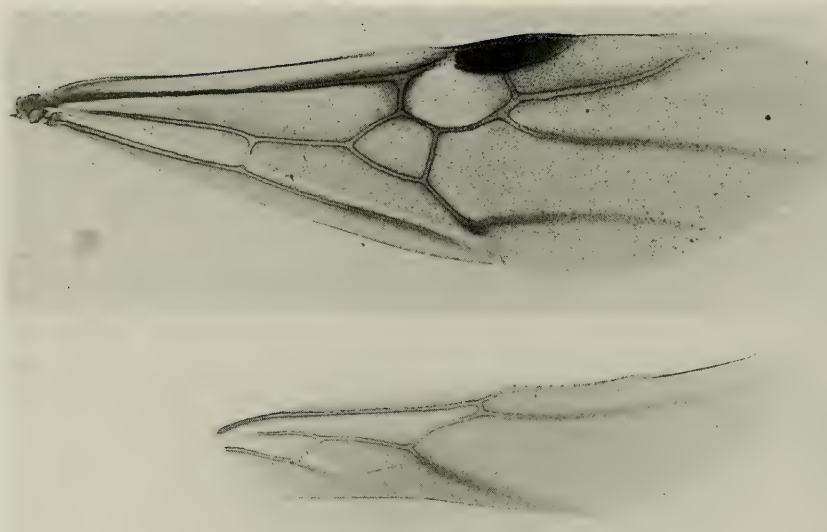


Fig. 161. *Cephalotes eduarduli* (FOREL). Gyne from Várzea Grande (Mato Grosso), Brazil, fore and hind wings .

reticulate-punctate and with small, superficial, piligerous punctures, the punctures deeper and denser on the anterior fourth of the first gastral tergite. Ventral part of the first gastral sternite shining. Legs reticulate and with piligerous punctures, the punctures denser on the extensor face of the femora and tibiae. Femora moderately shining on the sides.

Pilosity. Each fovea bears an appressed, canaliculate hair of size proportional to the one of the foveae; the hairs originating from the piligerous foveae thinner. Mandibles, sides of the head, trunk, peduncular segments, gaster and legs with slightly clavate, suberect hairs. Apex of the gaster with long, suberect, truncate hairs, similar hairs but sparser on the legs.

Colour. Black, gaster and legs lighter; frontal carinae, tarsomeres and extensor face of the tibiae dark ferruginous.

Measurements (in mm) and indices: TL 9.44–10.52; HL 1.78–2.00; HW 2.08–2.28; EL 0.48–0.52; PW 2.16–2.32; PeW 0.92–1.00; PpW 1.08–1.16; HBaL 0.67–0.73; HBaW 0.23–0.25; CI 112.0–117.8; PI 94.5–100.0; PPeI 216.0–247.8; PPpI 186.2–207.1; HBaI 34.2–35.2.

M a l e (Fig. 162). - Head (eyes included, mandibles excluded) about 1/3 broader than long; vertexal margin straight, superficially carinate and ending in two almost round, carinate angles. Ocelli protuberant. Vertex little convex. Eyes broadly convex, in the middle of the sides of the head. Frontal carinae raised, strongly converging anteriorly, diverging backwards and not reaching the posterior border of the eyes. Frons flat and separate from the clypeus by a superficial furrow. Clypeus convex, its posterior half higher than the anterior one, almost truncate. Mandibles slender, laterally carinate and with a distinct apical tooth. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view broadening backwards, superficially carinate on the sides and with marked scapular angles; mesonotum convex; median Mayrian carina and

parapsidal furrows weakly impressed; scutellum convex, its sides converging posteriorly; propodeum with poorly differentiate basal and declivous faces; basal face convex, its sides converging posteriorly towards the declivous face, the latter with lateral and median carinae.

Petiole slightly narrower than the postpetiole and with a deeply concave anterior border; petiolar sides convex medially or with a small, obtuse denticle. Postpetiole convex dorsally; postpetiolar sides with a pair of short, obtuse teeth in the middle.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 163.

Wings. As in the gyne.

Sculpture. Head and mesosoma deeply reticulate-punctate. Ventral part of the head with irregular and variably impressed, irregular rugulae; similar rugulae but more regular and transversal on the periocular area. Head and trunk with small, superficial, irregular foveae, the foveae smaller on the head, rare on the propleurae and absent on the metapleurae. Basal face of the propodeum with irregular rugosities becoming more regular on the metapleurae. Peduncular segments, first gastral tergite and sternite reticulate the reticulation more superficial on the legs and on the remaining gastral segments. Peduncular segments with few, thin, longitudinal rugosities.

Pilosity. Head and mesosoma covered by dense, long, suberect hairs, sparser and subdecumbent on the pedicel, on the gaster and on the legs. Funiculi densely covered by thin, short, decumbent hairs; similar but thinner, sparser and slightly longer hairs on the legs and on the gaster.

Colour. Head and mesosoma black, peduncular segments brown, first gastral segment ferruginous. Antennae, legs and remaining gastral segments yellow to light brown. Wings light ferruginous and infuscated.

Measurements (in mm) and indices: TL 6.12–6.88; HL 0.84–1.00; HW 1.16–1.36; EL 0.44–0.48; PW 1.16–1.32; PeW 0.60–0.68; PpW 0.68–0.76; HBaL 0.56–0.64; HBaW 0.12–0.14; CI 136.0–138.1; PI 100.0–103.0; PPeI 193.3–194.1; PPpI 170.6–173.7; HBaI 21.1–21.8.

Material examined. - **Brazil**: Pará: Tocantins, Itaguatins, 17–19. VII.1989, 3 workers, F. F. Ramos [MPEG]. Goiás: Jataí, XI.1972, 2 workers, F. M. Oliveira [MZSP]. Bahia: Itaberaba, Fazenda Riacho Uruçu, 05.XII.1990, 1 worker, C. R. F. Brandão, G. M. Diniz & P. S. Oliveira [MZSP]. Mato Grosso: no further locality, 1 soldier, Germain [MCSN]; Barra do Tapirapé, 13.I.1963, 2 workers, B. Malkin [MZSP]; Coxipó, 17.II.1976, 4 workers, R. L. Araújo [MZSP]; Município Várzea Grande, BR–070, km 530, 27.IX.1984, 6 workers, 12 soldiers, 1 gyne, 1 male, J. C. Trager [MZSP]; same locality and collector, 14.II.1985, 3 workers, 5 soldiers [MZSP]. Mato Grosso do Sul: Jardim, I.1962, 1 worker, R. Mueller [MZSP]; Três Lagoas, Fazenda Yamaguti, Cor. da Onça, VI.1964, 2 workers, 2 soldiers, Exp. Dep. Zool. [MZSP]. São Paulo: Agudos, VII.1954, VIII.1954, IX.1954, VI.1958, VII.1958, VIII.1958, IX.1958, 14 workers, R. Mueller [MCZC, MZSP]; same locality, 23.I.1955, 20.XI.1955, 3 workers, W. W. Kempf [MZSP]; Lençóis Paulista, VII.1969, 1 worker, R. Mueller [MZSP]; Avaré, Fazenda Guarujá, 22.IV.1972, 1 worker, F. Lane [MZSP]; Piracicaba, ESALQ, 540 m, 4 workers, 2 soldiers, E. Berti Filho [MZSP]; Boracéia, Mun. Itapui, VII.1960, 1 worker, R. Mueller [MZSP]; Castilho, left side of the Rio Paraná, 18.X.1964, 3 workers, 2 gynes, 2 males [MZSP]; Irapuã, 25.VII.1990, 1 worker, M. L. de Andrade [ZSMC]; Botucatu, 1 worker, M. L. de Andrade [NHMB]; Lins, 06.IX.1995, 5 workers, M. L. de Andrade [CCPC, INPA, MCZC, USNM].

Argentina: Chaco: Charata, 1 worker, 1 soldier, Bosq. [MZSP]. Misiones: Misiones, 02.I.1922, 2 workers, A. Zotta [MZSP].

Paraguay: La Cordillera: San Bernardino, 1 male, K. Fiebrig [MHNG]. Alto Paraná: Pastoreo, 18.IX.1974, 2 workers, 2 soldiers, P. Duelli [MZSP]. Concepción: Concepción, 26 workers, 18 soldiers, 10 gynes, (all syntypes), Chodat [MHNG].

Discussion. - The worker of *eduarduli* is easily differentiated from all the other species of the *depressus* clade by the presence of truncate hairs on the

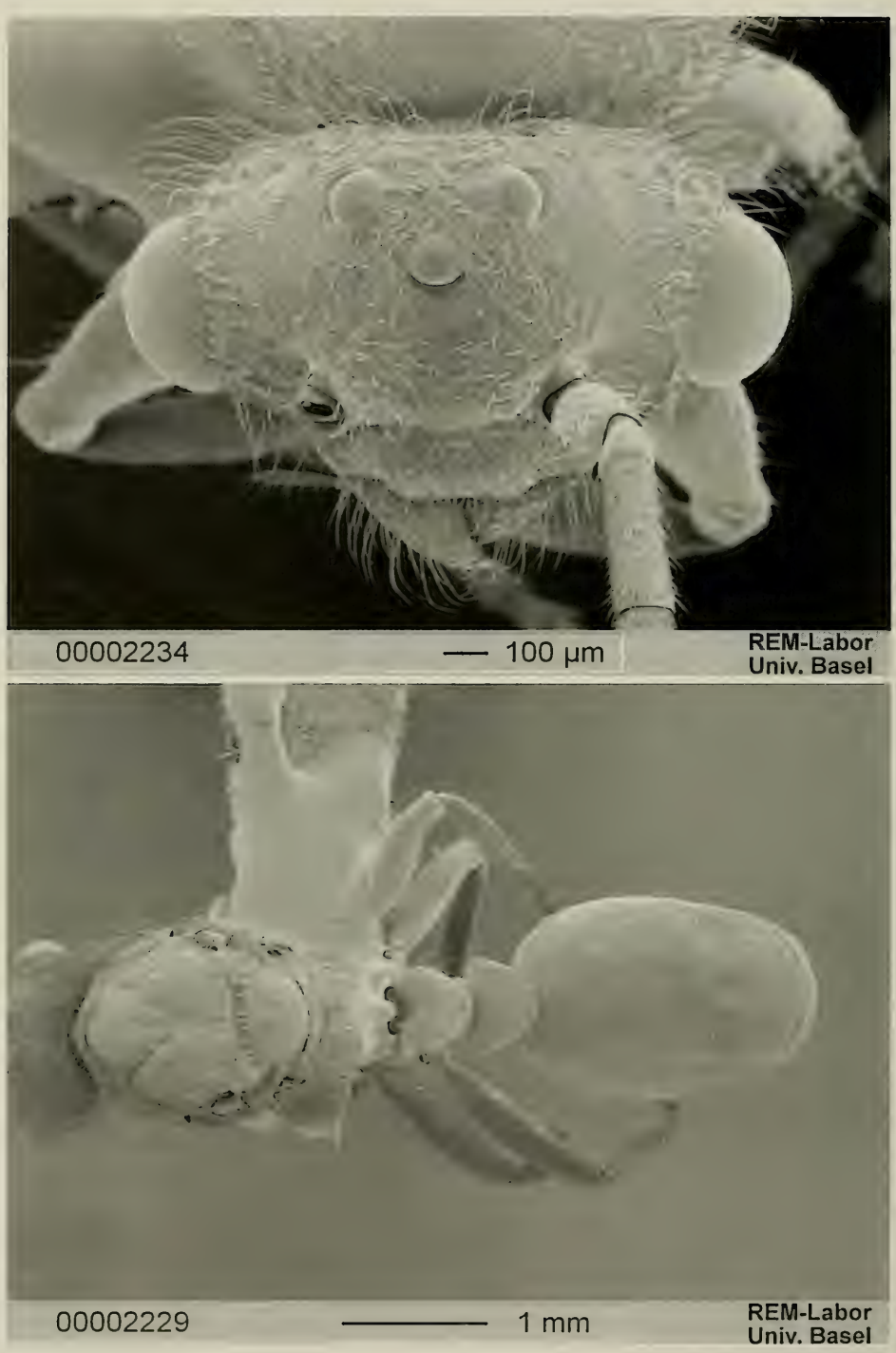


Fig. 162. *Cephalotes eduarduli* (FOREL). Male from Várzea Grande (Mato Grosso), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

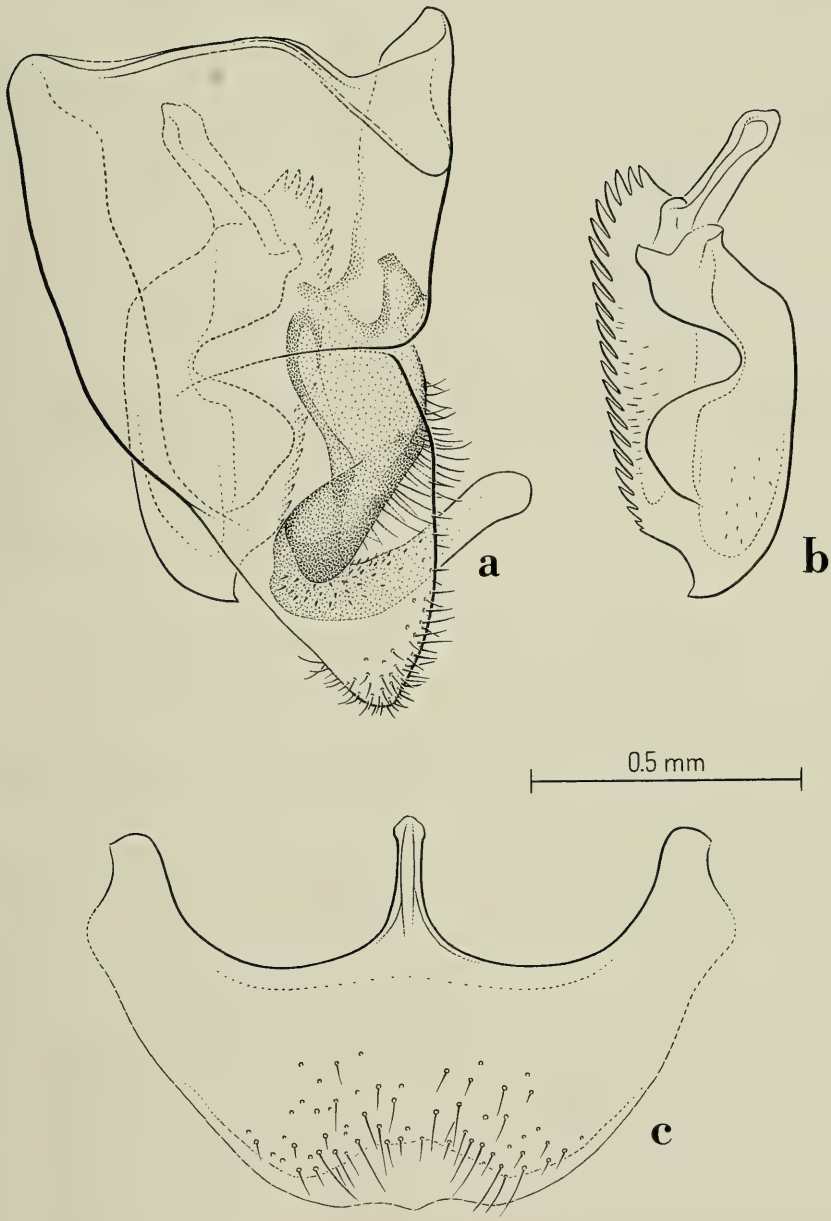


Fig. 163. *Cephalotes eduarduli* (Forel). Male from Castilho (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

mesosoma, pedicel and gaster. The soldier and the gyne of *eduarduli* also possess similar but fewer hairs on the mesosoma.

The shape of the gaster is subject to intranidal variability; it can be either oval or round according to the specimen. The soldiers from Mato Grosso do Sul (Fazenda Yamaguti) and the gynes from Castilho (S. Paulo) have the frontal carinae orange ferruginous and semi-transparent instead of reddish, darker and opaque.

Distribution: Brazil, Bolivia, Argentina, Paraguay.

5.6.10. The *umbraculatus* clade

As already intuitively proposed by EMERY (1922) and by KEMPF (1958) this is a very distinctive clade containing only one species characterised by the following five autapomorphies: characters 8: 0->2, 50: 0->1, 108: 0->1, 118: 0->1, 126: 0->1. In spite of the resulting isolate status within the *Cephalotes* phylogeny, *umbraculatus* shows some characters clearly intermediate between its most adjacent clades as listed under the discussion of the species. *Umbraculatus* appears to be one of the commonest species of the genus in large parts of the Neotropical rain forests.

Cephalotes umbraculatus (FABRICIUS) new combination
Figs. 164, 165,166

Cryptocerus umbraculatus FABRICIUS, 1804: 420. Worker. Original description. Type locality: „in America meridionali", actually Essequibo (Guyana). Type material: holotype worker in ZMUC, (ZIMSEN, 1964: 427) (examined), labelled „Essequibo, Smidt, Mus. J. Lund, *Cryptocerus umbraculatus* Fabr.".

Cryptocerus umbraculatus FABRICIUS, KLUG, 1824: 210. Gyne.

Cryptocerus quadriguttatus GUÉRIN-MÉNEVILLE, 1845: 425. Worker. Original description. Type localities: Colombia, Bolivia. Type material: not available for the present study. Synonymy by EMERY, 1890: 72.

Cryptocerus elegans SMITH, 1854: 222, pl. 19, fig. 3. Worker. Original description. Type localities: Colombia and Santarém (Brazil). Type material: two syntype workers in OXUM (KEMPF, 1959: 98), one syntype worker from Egas (=Tefé), Brazil, in BMNH, examined. Synonymy by EMERY, 1890: 72.

Cryptocerus flavomaculatus MAYR, 1862: 757. Gyne. Original description. Type locality: Brazil. Type material: not available for the present study. Synonymy by EMERY, 1890: 72.

Cryptocerus umbraculatus FABRICIUS, EMERY, 1890: 72, pl. 9, fig. 1 a-e. Soldier.

Cryptocerus umbraculatus FABRICIUS, FOREL, 1899 a: 51, pl. 3, figs. 1–16. Worker, soldier, gyne, male.

Paracryptocerus umbraculatus (FABRICIUS), SMITH, 1949: 20. First combination in *Paracryptocerus*.

Paracryptocerus umbraculatus (FABRICIUS), WHEELER & WHEELER, 1954 b: 156, figs. 42–44. Larva.

Paracryptocerus umbraculatus (FABRICIUS), KEMPF, 1958 a: 142, pl. 6, figs. 3, 9, pl. 7, figs. 1–5. Worker, soldier, gyne.

Zacryptocerus umbraculatus, HESPENHEIDE, 1986: Fig. 3. Worker. First combination in *Zacryptocerus*.

Diagnosis. - A member of its own clade characterised by the autapomorphies already listed in the clade description. In the worker, in the soldier and in the gyne, the combination of a three-segmented antennal club together with a transverse brown strip on the first gastral tergite should easily differentiate it from all the other species of the genus.

W o r k e r (description of KEMPF, 1958). - „Total length 5.3–6.2 mm; maximum length of head 1.43–1.68 mm; maximum length of thorax 1.57–1.82 mm. Basic color ochraceous in variable shades, the gaster with four light spots. Frequently the gaster, more seldom the thorax, are more or less heavily infuscated, the former may be entirely black, except for the light spots on the corners. Very rarely the entire insect is fuscous, including the gastral spots. Frontal carinae pellucid. Lateral portion of occipital border with a pellucid, crenulate crest. Vertex often with a pair of denticles. Lateral border of head very strongly upturned above eyes, forming on the inside on each side of dorsum of head, a deeply excavate longitudinal furrow. Scapular corner distinct, yet included in the foliaceus lateral pronotal crest, which contains also a stronger, foliaceous, projecting tooth, being slightly recurved at its apex. Sides of mesonotum usually with a minute foliaceous denticle. Mesoepinotal suture usually impressed. Lateral border of epinotum with a narrow, foliaceous, crenulate or even serrate crest. Hind femora, as seen in profile, angulate and dentate above near the middle. Petiole much longer than deep without a distinctly raised anterior face above the thoracic insertion. Lateral appendages of peduncular segments with foliaceous, often crenulate or serrate crests. Gaster between cordate and circular, remarkably short and broad, the anterolateral crests pellucid and prominent. Standing hair only on apex of gaster. Scalelike hair in foveolae of head, thorax and peduncle canaliculate and conspicuous, minute and fine on first gastral tergite."

Measurements (in mm) and indices: TL 5.73–6.44; HL 1.32–1.44; HW 1.68–1.86; EL 0.34–0.35; PW 1.36–1.52; PeW 0.76–0.84; PpW 0.80–0.88; HBaL 0.67–0.72; HBaW 0.18–0.22; CI 127.3–129.2; PI 122.4–123.5; PPeI 178.9–180.9; PPpI 170.0–172.7; HBaI 29.0–30.5.

S o l d i e r (description of KEMPF, 1958). - „Total length 7.6–8.0 mm; maximum length of head 2.32–2.46 mm; maximum length of thorax 2.18–2.42 mm. Color as in worker. Cephalic disc always broader than long, its lateral border upturned, the anterior portion of floor of disc shiny, the mesial portions subopaque, the posterior border scarcely raised and bidentate. Occipital lobes with crenulate and crested borders, a small carinule starting on the posterior corner running upwards to the border of the disc. Thorax broadest at the level of the sharply crested transverse pronotal carinae, the broadly expanded pronotum forming at this point a subacute angle. Sides of mesonotum with a small, crested, recurved, angulate lobe. Lateral border of basal face of epinotum finely crested, with a strong tooth on the posterior corner, which is strongly raised and upturned. Declivous face with the lateral borders beset with a foliaceous crest. Hind femora, peduncular segments and gaster similar to those of worker."

Measurements (in mm) and indices: TL 7.60–7.80; HL 1.92–1.96; HW 2.52–2.56; EL 0.37–0.38; PW 2.48–2.60; PeW 0.92–0.99; PpW 1.00; HBaL 0.72; HBaW 0.24; CI 128.6–133.3; PI 96.9–103.2; PPeI 250.5–282.6; PPpI 248.0–260.0; HBaI 33.3.

G y n e (Fig. 164) (description of KEMPF, 1958). - „Total length 10.0–11.0 mm; maximum length of head 2.64–2.71 mm; maximum length of thorax 3.18–3.25 mm. Resembling the soldier with the differences of the caste. Cephalic disc distinctly elongate and oval, excavate only above the frontal antennal scrobe, the rest moderately convex. Ocelli not far removed from the posterior border of disc. Borders of occipital lobes sharply crested and crenulate. Basal face of epinotum with a strong, diverging tooth on each of the posterior corners. Femora fusiform, not angulate above. Wings subhyaline, the apical half tinted with brownish, and the veins dark-brown. Venation of fore wing of the usual type, a transverse cubital vein (or vein *r-m*) being present."

Wings (Fig. 164): fore wings with *R+Sc* superficially connected with a marked pterostigma. *2r* marked, *Rsf5* connected with *R1*. Distal parts of *A*, *Cu-A* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; *CuA*, *M* and distal part of *1A* vestigial.

Measurements (in mm) and indices: TL 11.32–11.86; HL 2.24–2.36; HW 2.48–2.72; EL 0.44; PW 2.44–2.60; PeW 0.84–1.00; PpW 1.16–1.20; HBaL 0.96–104; HBaW 0.34; CI 110.7–115; PI 101.6–104.6; PPeI 260.0–290.5; PPpI 210.3–216.7; HBaI 32.7–35.4.

M a l e (Fig. 165) (already figured but not described by FOREL, 1889 a). - Head almost 1/3 broader than long (eyes included and mandibles excluded). Vertexal margin prolonging backwards as a „neck" and gently convex in full face view. Vertexal angles with superficially

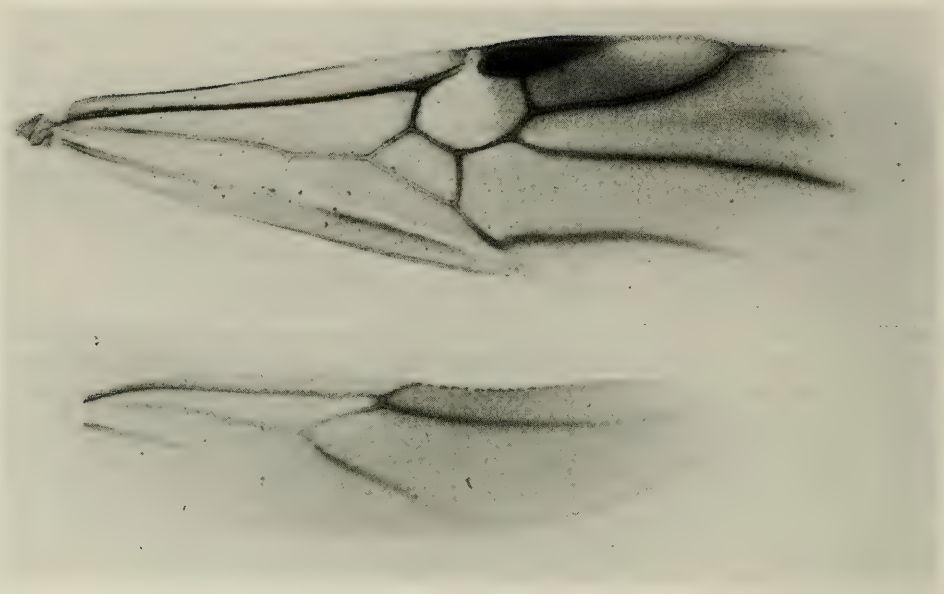


Fig. 164. *Cephalotes umbraculatus* (FABRICIUS). Gyne from Trinidad, fore and hind wings.

crenulate carina prolonging to the internal border of the eyes. Ocelli broad and protruding on the vertex. Eyes broadly convex, in the middle of the sides of the head, long one third of head length (mandibles included). Frontal carinae diverging backwards, interrupted at the level of the first ocellus. Frons flat. Clypeus medially convex. Mandibles slender, laterally carinate. Scapes thick, twice longer than the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Scapular angles long and well visible in dorsal view; pronotal sides parallel and bearing a crenulate carina; posterior part of the propleurae with a broad, concave dorsoventral sulcus hidden in dorsal view by the pronotal carina. Promesonotal suture deeply impressed and anteriorly marked by a thin pronotal carina. Mesonotum little convex in side view; pair Mayrian furrows broad and deeply impressed and median Mayrian furrow absent. Scutellum convex, its sides converging posteriorly. Propodeum with differentiate basal and declivous faces; basal face with a thin lateral lamina, slightly declivous, its sides converging posteriorly and laterally.

Petiole narrower than postpetiole, concave and declivous on the middle; its anterior border with a small denticle on each side; its sides moderately convex. Postpetiole dorsally little convex; its sides with a pair of small, obtuse denticles anteriorly.

Gaster heart-shaped.

Genitalia and subgenital plate as in Fig. 166.

Wings as in the gyne.

Sculpture. Head and mesosoma deeply reticulate and with irregular, deep foveae more regular on the mesonotum. Pedicel, gaster and femora reticulate, the reticulation more impressed on the first gastral tergite and on the femora. Remaining legs parts punctate only. Declivous face of the propodeum and propleural sulci almost shining.

Pilosity. Head, mesosoma, postpetiolar and gastral sternites, coxae and ventral face of the femora covered by long, sparse, suberect hairs, rare on the dorsum of the gastral tergites,

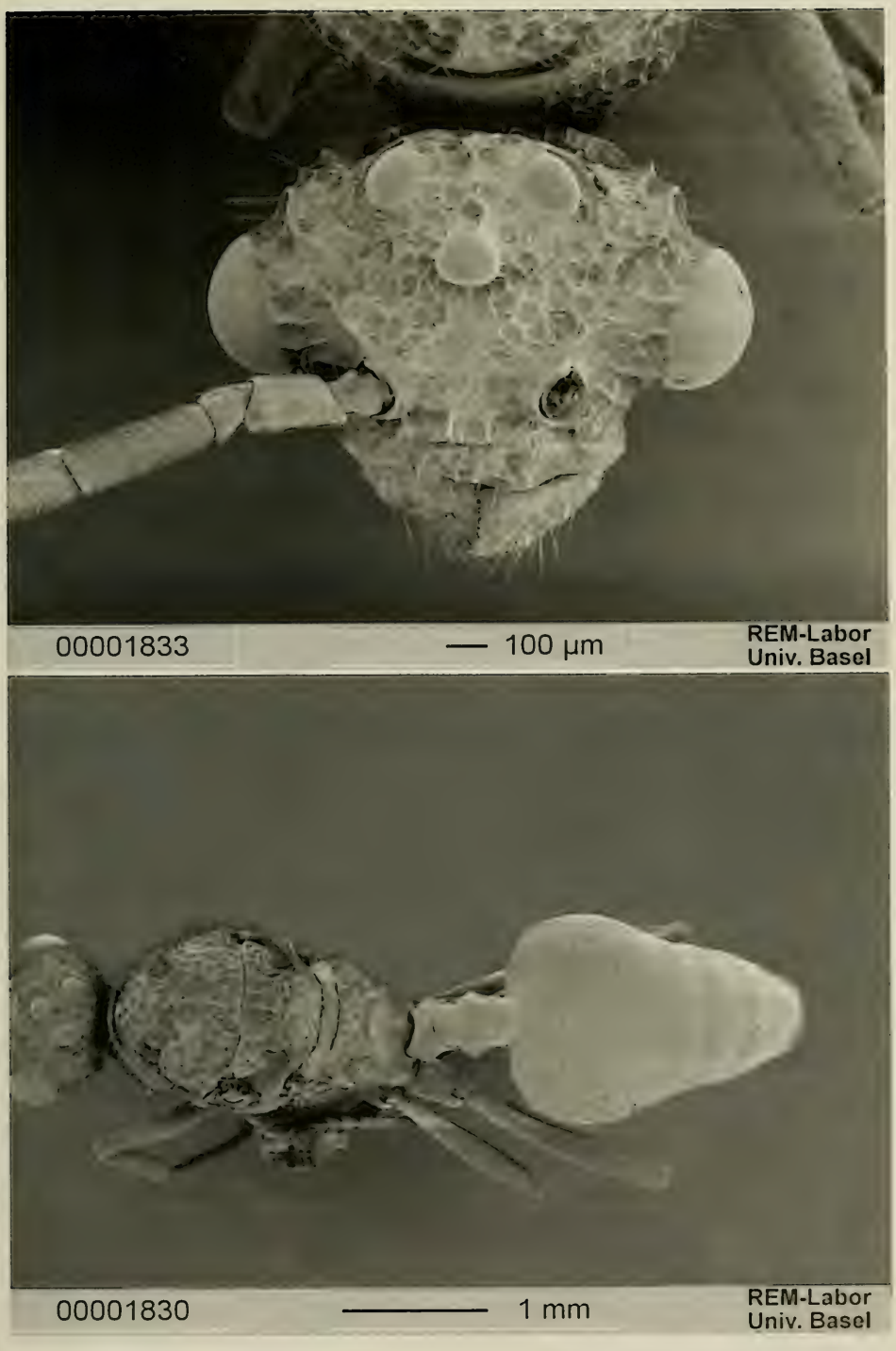


Fig. 165. *Cephalotes umbraculatus* (FABRICIUS). Male from Kartabo, Guyana: head (top) and meso- and metasoma (bottom) in dorsal view.

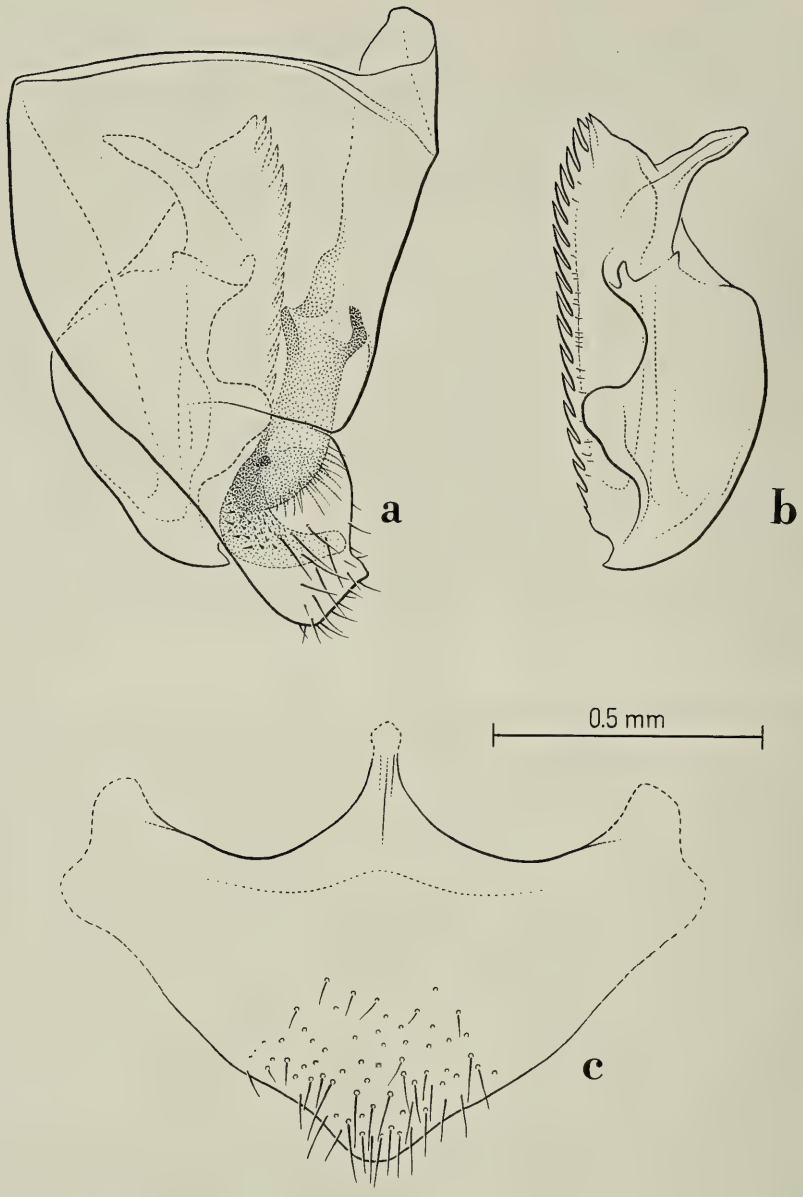


Fig. 166. *Cephalotes umbraculatus* (FABRICIUS). Male from Kartabo, Guyana. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

absent on the dorsum of the pedicel, of the femora and on the tibiae. Funiculi densely covered by thin, short, decumbent hairs, similar but thinner, sparser and slightly longer, subdecumbent hairs on the sides of the pedicel, appressed on the gastral tergites and sternites, on the dorsal face of the femora and on the tibiae and on the gaster.

Colour. Head and mesosoma black with lighter pedicel and first gastral segments; mandibles, antennae, legs and remaining gastral segments yellow.

Measurements (in mm) and indices: TL 5.68–6.12; HL 0.92–0.96; HW 1.04–1.08; EL 0.40; PW 1.04–1.08; PeW 0.42–0.44; PpW 0.54–0.52; HBaL 0.82–0.88; HBaW 0.12; CI 108.3–117.4; PI 96.1–100.0; PPeI 236.4–257.1; PPpI 200.0–240.0; HBaI 13.6–14.6.

Material examined. - **Mexico**: Guerrero: without further locality, 1 worker, W. U. Hapen [MCZC].

El Salvador: Prov. San Salvador, Lago de Ilopango, N side, 05.IV.1973, 1 worker, R. Silberglied [USNM].

Guatemala: Escuintla, 28–29.XII.1911, 19 workers, W. M. Wheeler [MCZC, MZSP]; Patulul, 08.I.1912, 4 workers, W. M. Wheeler [MCZC].

Costa Rica: no further locality, 3 workers [MHNG]; Alajuela, 1 worker, Alfaro [MCSN]; Bagaces, 2 soldiers [MCSN]; Prov. El Coco, 22.VII.1965, 2 workers, F. Coyle [MZSP]; Turrucarés, Jul. 1940, 2 workers, Bierig [MZSP]; Tempisque, 20.I.1937, 2 workers, A. Alfaro [MZSP]; Sirena, Penin. Osa, Par. Nat. Corcovado, 8°28' N, 83°35' W, 0–100 m, 8.VIII.1982, 1 worker, 1 soldier, J. Longino [MCZC]; Ojo de Agua, 06.X.1929, 16 workers, 2 soldiers, A. Alfaro [MCZC, USNM].

Panama: Pueblo Nuevo, Jun. 1930, 1 worker, Bierig [MZSP]; Barro Colorado, Gatun Lake, 17.VII.1923, 2 workers, R. C. Shannon [USNM]; Barro Colorado Island, Canal Zone, 7 workers, W. C. Allee [MCZC]; Barro Colorado Island, Canal Zone, 12 workers, 2 soldiers, W. M. Wheeler [MCZC, USNM]; same locality and collector, 20.6.1924, 4 workers, 1 soldier [MCZC]; same locality and collector, 21–24.VI.1924, 4 workers, 3 soldiers, [MCZC]; same locality, 10.V.1976, 1 gyne, 1 male (in copula), Silberglied & Aiello [MCZC]; Red Tank, Canal Zone, 6 workers, 1 soldier, W. M. Wheeler [MCZC]; Tolé, 2 workers [MHNG]; Mt. Hope nr. Colon, Canal Zone, 49 workers, 6 soldiers, W. M. Wheeler [MCZC].

Colombia: Magdalena: Río Frío, 26.II.1928, 1 worker, Darlington [MZSP]; same locality, 04.VIII.1928, 2 workers, Darlington [MCZC]. Meta: Carimagua, 28.V.1973, 370 m, 11 workers, 1 soldier [MZSP]; Res. Nac. Nat. La Macareña, Caño, La Curia, 580 m, 06.I.1987, 1 worker, F. Fernández [MZSP].

Venezuela: Nueva Esparta: Margarita Island, La Valle, II.1974, 1 worker, A. Dennison [MCZC].

Trinidad & Tobago: Trinidad: no further locality, 1 gyne, 1 male [MCSN]; no further locality, 24 workers, 7 soldiers, 6 gynes, 4 males, Urich [MHNG, NHMB]; Nariva, 23.IV.1935, 1 worker, N. A. Weber [MCZC]; Port of Spain, 3 workers, Wheeler [MCZC]; St. Augustine, 16.XI.1934, 7 workers, 3 gynes, N. A. Weber [MCZC]; Mayaro, 28.IV.1929, 1 worker, Darlington [MZSP]. Tobago: St. John Prov., Hermitage River Bridge, Charlotteville, 12–21.III.1979, 1 worker, D. Hardy & W. Rowe [USNM].

Guyana: Essequibo: no further locality, 1 worker (holotype), Smidt [ZMUC]; Kartabo, Jul.-Aug. 1920, 6 workers, 4 soldiers, 5 workers, W. M. Wheeler [MCZC]; Forest Settlement, 25.VIII.1935, 3 workers, N. A. Weber [MCZC].

Surinam: Paramaribo, 1 worker, Buenzli [MZSP].

French Guyana: St. Jean, 1 gyne, Wm. Schaus [MCZC].

Brazil: Amazonas: no further locality, 2 workers, H. W. Bates [ZSMC]; Manaus to Itacoatiara, highway, km 15, 07.VI.1971, 4 workers, W. L. Brown & D. E. Brown [MCZC]; Manaus, Col. Sto. Antônio, 02.VI.1971, 11 workers, 4 soldiers [MZSP]; Rio Prêto da Eva, 13–15.VI.1967, 7 workers, Exp. Perm. Amazonas [MZSP]; Humaitá, 23.VI.1975, 3 workers, 1 soldier, V. P. Silva, Araujo & Dillon [MZSP]. Pará: Serra Norte, Manganês, 6.V.1984, 1 worker, T. Pimentel [MPEG]; Serra Norte, N1 mata, 28–31.X.1985, 1 worker, W. França [MPEG]; Serra Cipó Pitanga, low Rio Xingú, 30.XI.1983, 1 worker [MPEG]; Belém, 1 worker, E. Dente [MZSP]; Rio Cuminá, 1928, 1 worker, Sampaio [MZSP]; Boca do

Cuminá-Miri, 20.I.1968, 4 workers, Exp. Perm. Amazonas [MZSP]; Cachoeira do Breu, Oct. 1928, 2 workers, SAMPAIO [MZSP]. Rio Grande do Norte: Goianinha, 14.X.1951, 2 workers, M. ALVARENGA [MZSP]. Acre: Abunã, Rio Madeira, 6 workers, 3 soldiers, 2 gynes, 2 males, MANN & BAKER [MCZC]. Rondônia: 5 km SW Santa Cruz da Serra, 04–10.XI.1985, 1 worker, MZ-Polonoroeste [MZSP]. Goiás: Jataí, Dec. 1972, 1 worker, F. M. OLIVEIRA [MZSP]. Mato Grosso: Sinop, 55°37'W 12°31'S, Oct. 1974, 1 soldier [MZSP]; Utiariti (325 m), Rio Papagaio, Jul.-Aug. 1961, 25 workers, K. LENKO [MZSP]; Utiariti (325 m), Rio Papagaio, 01–06.XI.1966, 15 workers, K. LENKO & V. P. SILVA [MZSP]. Bahia: Ilhéus, CEPEC, 20.IV.1993, 3 workers, 1 soldier, M. FÜRST [CPCC]. Espírito Santo: Vila Velha, Convento da Penha, I.1954, 1 worker, R. MUELLER [MZSP].

Peru: Valle Chanchamayo, 800 m, 01.VIII.1939, 1 worker, 1 soldier, WEYRAUCH [MZSP]; Chanchamayo, 1 gyne [MCZC]. Lima: Lima, Andes Mts, 1914, 1 soldier, W. M. WHEELER [MCZC].

Bolivia: no further locality, 1 soldier, STAUDINGER [MCSN]. Beni: Río Beni, Salinas, 1891, 15 workers, BALZAN [MCSN]; Rurrenabaque, IX.1921, 2 workers, W. M. MANN [MZSP]. La Paz: Tumupasa, XII.1921, 1 worker, 1 soldier, 1 gyne, W. M. MANN [MZSP]; Ixiamas, XII.1921, 1 worker, 1 soldier, 1 gyne, M. R. LOPES [MZSP]. Santa Cruz: Yapacani, 10.VIII.1965, forest, 9 workers, J. D. CANDIA [MCZC].

Discussion. - *C. umbraculatus* shares characters with species of the *depressus*, of the *multispinosus* and of the *grandinosus* clades. The worker shares with the species of the *depressus* and *multispinosus* clades the flat petiole and the propodeum making with the anterior face of the petiole in relaxed position an angle > 110°. The male has a deep concavity on the internal border of the aedeagus, a character in common with all males of the *depressus* clade we dissected. The gyne shares with the gynes of the *grandinosus* clade the transverse brown strip on the first gastral tergite.

Umbraculatus is normally yellowish to light brown, but there are darker specimens with a dark brown gastral spot or strip.

FERNÁNDEZ et al. (1996) report this species also from the Colombian states of Amazonas, Antioquia, Bolívar, Chocó, Huila, Nariño, Tolima and Caquetá.

Distribution: Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Panama, Colombia, Venezuela, Trinidad, Tobago, Guyanas, Brazil, Peru, Bolivia.

5.6.11. The *pinelii* clade

This is a medium sized clade containing nine species, including one fossil in Dominican amber. Both its known unequivocal synapomorphies are chromatic, i. e. two coloured spots or strips on the gaster of the worker and four coloured spots on the gaster of the gynes. However weak these characters may appear, they are likely to have a clear, probably aposematic, adaptive meaning. Similar colour patterns are known also in members of the *multispinosus*, *bimaculatus*, *coffeae* and *angustus* clades. The *pinelii* clade, however, is distantly related to all of them for possessing membranaceous expansions on the mesosoma (absent in all members of the aforementioned four clades) and for the antennal club two-jointed (three-jointed in the *multispinosus*, *coffeae* and *angustus* clades). The *pinelii* clade as we define it in this paper is much narrower than the „*pinelii* complex" previously recognised by EMERY (1922) and by KEMPF (1952). As already noted by KEMPF (l. c.) most of these species occasionally nest in epiphytes.

Species included in the clade: *caribicus*, *incertus*, *kukulcan*, *liepini*, *maculatus*, *nilpiei*, *pileini*, *pinelii*, *scutulatus*.

Cephalotes maculatus (SMITH) new combination

Figs. 167, 384 B

Cryptocerus maculatus SMITH, 1876: 607, pl. 11, fig. 6. Gyne. Original description. Type locality: Salvador (Bahia, Brazil). Type material: Holotype gyne labelled „Bahia" in BMNH, examined.

Cryptocerus maculatus SMITH, EMERY, 1894 a: 208, figs. 18–21. Worker, soldier.

Cryptocerus maculatus SMITH, FOREL, 1905: 158. Male.

Cryptocerus grandinosus magdalenensis FOREL, 1899 b: 303, fig. without number. Worker. Original description. Type locality: Colombia (San Pablo, Magdalena R., specified by FOREL, 1899 c: 275). Type material: holotype worker labelled „*Cr. grandinosus* r. *magdalenensis*, For., type, San Pablo and Magdalena, Colombie, in ZSMC (examined). New synonymy.

Cryptocerus maculatus nanus FOREL, 1912: 202. Worker. Original description. Type locality: Trinidad (savannah). Type material: 1 worker labelled: „*Cr. maculatus* Sm., R. *nanus*, type Forel, Savanne, Trinidad (Forel)", in MHNG, examined. Synonymy tentatively proposed by KEMPF (1952: 19) and confirmed in this paper.

Cryptocerus maculatus SMITH, MENOZZI, 1927: 336, fig. 3. Male.

Paracryptocerus maculatus (SMITH), KEMPF, 1952: 18, figs. 5, 7, 11, 14. Worker, soldier, gyne. First combination in *Paracryptocerus*.

Paracryptocerus grandinosus (SMITH), KEMPF, 1952: 11. Partim. Nec SMITH, 1860. Misidentification.

Paracryptocerus maculatus (SMITH), WHEELER & WHEELER, 1954 b: 156. Larva.

Zacryptocerus maculatus (SMITH), HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *pinelii* clade differing from all the other species of the clade in the worker by the maximum diameter of the eyes greater than 1/3 of the head length, in the soldier, by the flat vertex, in the soldier and in the gyne by the concolour head and pronotum.

Worker (Fig. 167) (description of KEMPF, 1952). - „Length 2.6–3.0 mm. Fuscous reddish-brown to black. Outer face of tibiae pale brown. Rest of legs ferruginous. Frontal carinae and membranaceous borders of thorax, peduncle and gaster whitish.

Head subquadrate, longer than wide, the median head length as long as, or longer than, the interocular width. Edge of lateral border smooth. Sides of head slightly convex and upturned above eyes. Occipital corner little or not membranaceous, sharply angulate to subdentate. Occipital border straight. Greatest diameter of eyes almost one third of maximum head length.

Thorax longer than wide. Membranaceous border of pronotum and epinotum broad, not forming a reentrant angle at the mesonotum. Shoulders subacutely angulate. Sides of mesonotum with a small projecting tooth, the tip of which is often membranaceous. Mesoepinotal suture distinct. Declivous face of epinotum differentiated from the basal face. Dorsum of hind femora longitudinally marginate, not crested, on the apical half; no crest on the lower face.

Peduncular segments subequal in width to the width of the epinotum, with conspicuous lateral membranaceous appendages. Anterior face of petiole usually notched mesally.

Gaster longer than wide, proportionally shorter than in *pinelii* and *grandinosus*. Anterolateral membranaceous border rounded.

Subopaque, finely shagreened. Dorsum of head, thorax and peduncle with small squamiferous foveolae. Dorsum of thorax, especially on the region of the mesoepinotal suture usually with distinct longitudinal rugosities. Sides of thorax, except the laterotergite of the

Fig. 167. *Cephalotes maculatus* (SMITH). Worker from Arriago (Chiapas), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

pronotum, and the declivous face longitudinally striated. Scale-like hair small, shiny, appressed. No erect setae on the first gastral tergite."

Measurements (in mm) and indices: TL 2.81–3.93; HL 0.70–0.92; HW 0.78–1.00; EL 0.25–0.31; PW 0.72–0.96; PeW 0.50–0.59; PpW 0.48–0.56; HBaL 0.18–0.26; HBaW 0.06–0.09; CI 108.7–111.4; PI 104.2–108.3; PPeI 144.0–162.7; PPpI 150.0–171.4; HBaI 33.3–34.6.

S o l d i e r (Fig. 384 B) (description of KEMPF, 1952). - „Length 3.9–4.2 mm. Color as in worker. Head disc uniformly fuscous reddish-brown to black, the portion overlying the antennal scrobe not membranaceous nor differently colored. First gastral tergite, especially in larger specimens, with lighter yellowish-brown spots, one toward each corner, the anterior pair often fusing mesally into a transverse band, the posterior pair usually small, somewhat removed from the posterior border.

Head slightly longer than wide; disc not well rounded, subrectangular, excavate, flat to scarcely convex mesally. Supramandibular excision subsemicircular. Border of disc not glassy nor membranaceous. Occipital border of cephalic disc usually straight and without a pair of small, projecting denticules. Sides of head continuous with the truncate occiput, not separated by a margination or ridge.

Thorax as long as wide across the pronotum. Anterior border of pronotum broadly excised laterad, the shoulders acute and spine-like. Transverse pronotal carina slightly interrupted mesally. Mesonotum much narrower than pronotum, with a projecting, usually angulate lobe on each side. Basal face of epinotum with a small rounded lobe laterally and an upturned tubercular tooth on each posterior corner. Sides of declivous face narrowly crested. Hind femora without a dorsal and ventral crest on the apical half.

Peduncular segments as in worker; the lateral membranaceous appendages less prominent.

Gaster elliptical. The anterolateral lobes rounded, the crests lacking in large soldiers.

Integument opaque, finely shagreened. Head disc coarsely and densely foveolate. The foveolae are much smaller on the dorsum of the thorax and the peduncular segments. Gaster and sides of thorax without any conspicuous foveolae. Scales as in worker, absent on the declivous face."

Measurements (in mm) and indices: TL 3.76–4.86; HL 0.96–1.20; HW 1.04–1.28; EL 0.28–0.30; PW 1.04–1.32; PeW 0.51–0.64; PpW 0.51–0.68; HBaL 0.24–0.28; HBaW 0.08–0.10; CI 106.7–108.3; PI 97.0–100.0; PPeI 203.9–206.2; PPpI 194.1–203.9; HBaI 33.3–35.7.

G y n e (description of KEMPF, 1952). - „Length 5.6–6.4 mm. Color as in soldier. The four maculae of the first gastral tergite better delimited and usually more prominent than in soldier, yellowish to ferruginous-yellow.

Head elongate, one and one fourth times as long as wide. Supramandibular excision narrow, subsemicircular. Cephalic disc elongate, subrectangular, moderately convex, slightly excavated, but not membranaceous, above the antennal scrobe; the sides subparallel, scarcely curved, often somewhat converging caudad; the edges of the disc scarcely crenulate, very little upturned, forming only a slightly prominent ridge postero-laterally above the occipital lobes.

Thorax elongate. Anterior border of pronotum somewhat excised laterally, not quite as prominent as in soldier. Shoulders acute. Transverse pronotal carina ininterrupted. Lower plate of mesopleura anteriorly with a tooth. Basal face of epinotum with a rounded lateral lobe and a rather sharp tooth on the posterior corner. Hind femora neither crested nor angulate above near the middle.

Peduncular segments massive, with the lateral projections scarcely membranaceous. Petiole with a lateral small tooth, pointing obliquely caudad, the postpetiole with a lateral obliquely truncate lobe, similar to that of soldier.

Gaster with the anterior border deeply emarginate, the anterolateral lobes rounded to subangulate.

Sculpture and pilosity as in soldier. The scales of the gaster are glistening and minute.

Wings hyaline. The venation of the fore wing of the usual pattern: a close and appendiculate marginal cell; transverse cubital vein present."

Measurements (in mm) and indices: TL 5.64–6.84; HL 1.20–1.28; HW 1.08–1.22; EL 0.29–0.32; PW 1.06–1.14; PeW 0.44–0.51; PpW 0.60–0.68; HBaL 0.33–0.35; HBaW 0.10–0.11; CI 90.0–95.3; PI 101.9–107.0; PPeI 223.5–240.9; PPpI 167.6–176.7; HBaI 30.3–31.4.

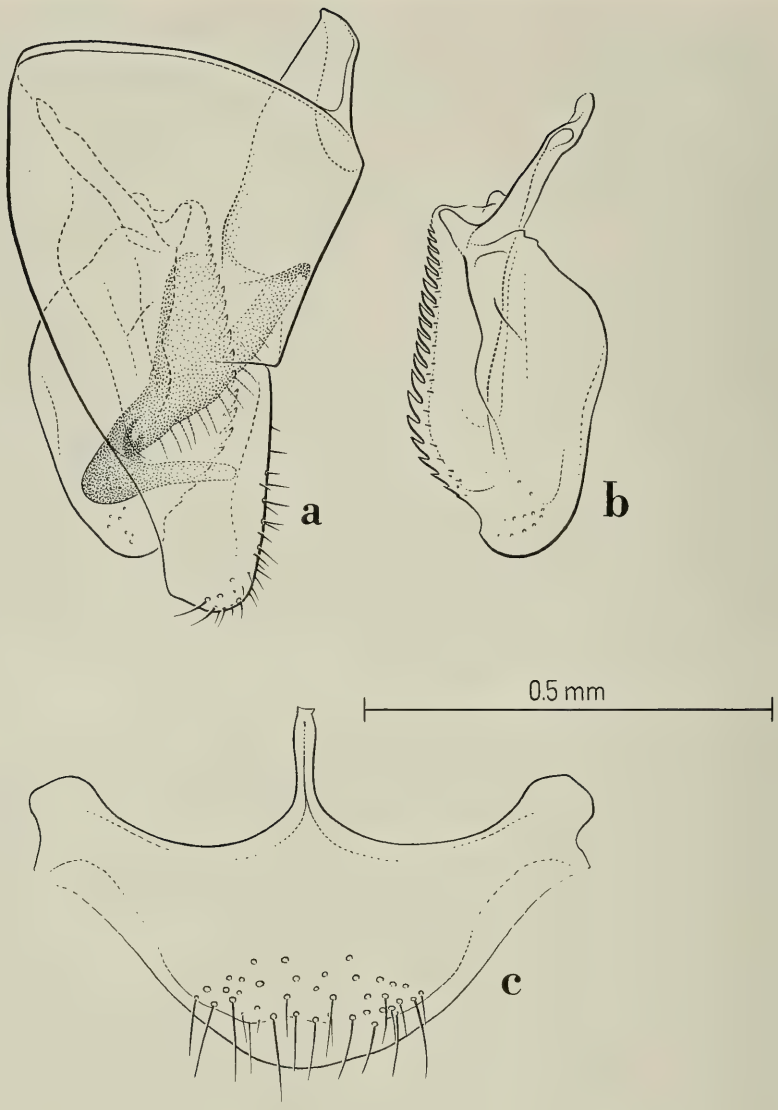


Fig. 168. *Cephalotes maculatus* (SMITH). Male from Las Cumbres, Panama. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

M a l e (translation of the description of MENOZZI, 1927). - „Black, antennae, tibiae and tarsi ferruginous. Abundant pilosity over the whole body; pubescence limited to the antennae, tibiae and tarsi. Head much wider than long, opaque, striate-punctate, except a transversal part between the eye and the frontal lamina, smooth and shining. Mandibles small, finely punctate, with the masticatory border armed with several very small teeth. Clypeus equally very small and strongly convex posteriorly. Antennae with very short scape; the first funicular joint one third of the second in length, the latter being the longest; the last joints twice as long as broad, and, beginning from the tenth, they broaden gradually up to the last, forming a club. Thorax with pronotum and mesonotum sculptured as the head but the striae constitute the

dominant pattern, particularly on their sides; scutellum simply punctate or, rarely, with two or three striae; metanotum and epinotum with visible rugae more or less curved on the dorsum, markedly straight on the sides. Mesonotum with deep Mayrian furrows. Basal face of the epinotum as long as the declivous one to which it is joined by an obtuse angle.

Petiole punctate, subquadrate and slightly marginate on the sides; postpetiole nearly shining, finely reticulate, slightly larger than the petiolar node, equally marginate on the sides which bear two small tubercles anteriorly. Gaster with sculpture similar to the one of the postpetiole, with the basal segment pyriform and occupying more than half of the whole gaster. Genitalia testaceous, with stipes broad and distally hairy; volsella terminating in a long hook with the lacinia built as a short lobe, partly concealed by the volsella itself. Wings hyaline with iridescent reflexes; pterostigma and veins testaceous; one cubital and one closed, not appendiculate radial cell, at least in the six males available to me. Length 5.2–5.8 mm."

Genitalia and subgenital plate as in Fig. 168.

Measurements (in mm) and indices: TL 3.31–4.41; HL 0.54–0.65; HW 0.67–0.82; EL 0.31–0.38; PW 0.54–0.68; PeW 0.27–0.33; PpW 0.25–0.32; HBaL 0.29–0.31; HBaW 0.05–0.06; CI 124.1–126.1; PI 120.6–124.1; PPeI 200.0–206.1; PPpI 212.5–216.0; HBaI 17.2–20.0.

Material examined. - **Mexico**: Chiapas: Arriago, 07.XII.1951, 25 workers, 3 soldiers, FOUTS [USNM].

Guatemala: Zacapa, 13 & 15.XII.1911, 6 workers, Wm. M. WHEELER [MCZC].

Honduras: Progresso, 1 worker, W. M. MANN [USNM].

Nicaragua: Managua, XI.1959, 1 worker, N. L. H. KRAUSS [USNM].

Costa Rica: no further locality, 22.I.1938, in *Cordia alliodora*, 7 workers, 1 soldier, F. NEVERMANN [MZSP]; Orotina, 07.XII.1929, 1 worker, 3 soldiers, A. ALFARO [MZSP]; Matina, 02.VIII.1936, 1 worker, 2 soldiers, 2 males, A. ALFARO [MZSP]; Alajuela, May 1896, in dry spines of *Acacia spadicigera*, 17 workers, 5 soldiers, 3 gynes, 1 male, ALFARO [MCSN]; same locality, 28.XI.1911, 1 worker, 1 soldier, W. M. WHEELER [MCZC]; Bagaces, 1 worker [MCSN]; San José, 1940, 3 workers, 1 soldier, H. SCHMIDT [MZSP]; same locality, 01.XII.1911, 5 workers, 1 soldier, 2 gynes, W. M. WHEELER [MCZC]; same locality, 3.5 km NE Santiago de Pur., 03.VII.1963, 1 worker, 1 soldier, D. H. JANZEN [USNM]; Cartago Prov. Turrialba, 18.VII.1965, 2 workers, 1 soldier, F. COYLE [MZSP]; Hamburg Farm, Reventazón, Ebene Limón, 4 workers, 4 soldiers, 1 gyne, 2 males [MZSP]; same locality, 15 workers, 4 soldiers, 2 males, F. NEVERMANN [MCZC, MZSP]; Ojo de Agua, 08.IX.1929, 1 worker, 1 soldier, A. ALFARO [MCZC].

Panama: Barro Colorado, 02.VII.1921, 1 worker, 1 soldier, G. L. WHEELER [NHMB]; same locality, 21–24.VI, 18.VII.1924, 9 workers, 1 soldier, N. BANKS [MCZC]; same locality, 2 workers [MZSP]; same locality, Univ. Chicago, 1 soldier, W. C. ALLEE [MCZC]; Las Cumbres, 09.XII.1982, 1 worker, 1 soldier, 2 gynes, 2 males, D. E. WHEELER [MCZC]; Ancon, 12.IV.1935, 2 workers, A. EMERSON [MCZC].

Colombia: Risaralda: Pereira, 1000 m, V.1975, 1 worker, A. J. NEGRETT [MZSP]. Magdalena: San Pablo, 1 worker (holotype of *magdalenensis*) [ZSMC]. Sucre: Sucre, Sincé, 09.X.1975, 5 workers, 4 soldiers, F. SCHREMMER [MZSP]. Cundinamarca: Río Sumapaz, Gorge E of Melgar, 05.I.1959, 1 worker, J. F. G. CLARKE [USNM]. Valle: SW of Cali, above Barrio Siloé, 14.VII.1972, 2 workers, 1 gyne, M. L. CORN [MZSP]. Amazonas: 35 km above Leticia, 40 m, 16.IX.1973, 1 gyne, M. L. CORN [MZSP].

Trinidad & Tobago: Trinidad: no further locality, 1 worker, 1 soldier [MCSN]; no further locality, 2 workers, 1 soldier, ULRICH [MHNG, NHMB]; Savannah, 1 worker (holotype of *nanus*), FOREL [MHNG]; Montserrat, 04.VII.1906, 1 worker, A. BUSCK [USNM]; St. Augustine, 20–30.IV.1929, 1 gyne, DARLINGTON [MCZC]; same locality, 28 & 29.XI.1934, 1 worker, 1 gyne, N. A. WEBER [MCZC]; Nariva Swamp, 05.XII.1934, 4 workers, 3 soldiers, 2 males, N. A. WEBER [MCZC]; Mayaro Bay, 04.XII.1934, 1 worker, N. A. WEBER [MCZC]; Arima Forest Reserve, S of Arima, 12.XII.1934, 1 gyne [MCZC]; Balandra Bay, E Coast, 26.XI.1934, 3 workers, N. A. WEBER [MCZC]; same locality, 26.XI.1937, 1 soldier, N. A. WEBER [MCZC]; North Range, El Tucuche, 15.XII.1935, 3 workers, WEBER [MCZC]; nr. Peter's Hall, 2 mi from Georgetown, 22.IX.1918, 2 workers, H. MORRISON [USNM]; Bot. Garden Georgetown, 26.IX.1918, 1 worker, H. MORRISON [USNM].

Venezuela: no further locality, 18.04.1941, intercepted in Brownsville, in *Cattleya mosside*, pseudobulb, 3 workers [MZSP]; no further locality, 06.VIII.1946, intercepted in Hoboken, on *Cattleya* pseudobulb, 1 worker [USNM]; Orinoco Delta, 31.I.1935, 3 workers, N. A. WEBER [MCZC]. Monagas: Barrancas, Jan.-Feb. 1935, 4 workers, N. A. WEBER [MCZC]. Bolívar: Las Trincheras, 5 workers, 2 soldiers, 3 gynes, 3 males, MEINERT [MHNG]; Ciudad Bolívar, 30.I.1935, 1 worker, N. A. WEBER [MCZC].

Guyana: Essequibo: Kartabo, Jul. Aug. 1920, 39 workers, 4 soldiers, 3 gynes, W. M. WHEELER [MCZC, MZSP]; Upper Essequibo, 01.XII.1935, 2 workers, J. G. MYERS [MCZC].

French Guyana: Cayenne, 5 workers, P. JANET [MCSN].

Ecuador: Morona Santiago: Los Tayos, 03.VIII.1976, 1 worker, T. VRIES [MZSP].

Brazil: Amapá: Highway BR. 156, km 14, border of Rio Matapi, 31.XI.1981, 1 worker [MPEG]. Amazonas: no further locality, 2 workers, H. W. BATES [ZSMC]; Res. Fl. A. Ducke, 2°55' S, 59°59'W, 18 & 23.XII.1981, 15 & 28.VII, 13 & 26.VIII, 30.IX, 12 & 29. XI.1982, 05.I.1983, 14 workers, 1 gyne, ADIS et al. [INPA]. Pará: Jacareacanga, XII.1968, 1 worker, M. ALVARENGA [MZSP]; São João de Pirabas, Japerica, 16–22.XII.1992, 4 workers, J. DIAS [MPEG]; Serra Norte, Campo Rupestre, 2–9.IX.1983, 2 workers, M. P. TORRES & R. B. NETO [MPEG]; Santarém Novo, Fazenda Jaburu, 7–9.I.1993, 1 worker, J. DIAS [MPEG]; Tocantins Itaguatins, 17–19.VII.1989, 1 soldier, F. F. RAMOS [MPEG]; Igarapeaçú, I.1949, 1 worker, GONÇALVES [MZSP]; Capanema, 09.I.1949, 2 workers, GONÇALVES [MZSP]; Carajás, Serra Sul, 21.VII.1985, 1 worker, C. R. F. BRANDÃO [MZSP]; Caldeirão, R. Itacaiunas, VII-VIII.1985, 1 gyne, C. R. F. BRANDÃO & W. BENSON [MZSP]. Ceará: no further locality, 3 workers, 3 gynes, ROCHA [MHNG]. Rio Grande do Norte: Natal, 1 gyne, W. M. MANN [USNM]; same locality, I.1952, 1 worker, M. ALVARENGA [MZSP]. Pernambuco: Caruarú, 30.XI.1927, 8 workers, 2 soldiers, 2 males, O. S. B. PICKEL [MZSP]; same locality, IV.1972, 1 gyne, ALVARENGA [MZSP]. Acre: Rio Branco, 25.X–8.XI.1981, 1 worker, F. RAMOS et al. [MPEG]. Rondônia: Forte Príncipe da Beira, 19.XI–03.XII.1962, 1 gyne [MZSP]. Goiás: Alto Paraiso, Fazenda Bona Espera, 2 workers, 1–7.VII.1991, C. R. F. BRANDÃO et al. [MZSP]. Mato Grosso: no further locality, 1886, 3 workers, 3 soldiers, P. GERMAIN [MCSN, MHNG]; Barra do Tapirapé, 21.XII.1960, 1 worker, B. MALKIN [MZSP]; Utiariti, Rio Papagaio, VII.1961, 2 workers, K. LENKO [MZSP]; same locality, 04.XI.1966, 31 workers, 17 soldiers, 7 males, LENKO & PEREIRA [MZSP]. Mato Grosso do Sul: Três Lagoas, Córrego da Onça, Fazenda Yamaguti, VI.1964, 34 workers, 5 soldiers, Exp. Dep. Zool. [MZSP]; same locality, Fazenda Dr. José Mendes, 26.V.1964, 3 soldiers, 5 gynes, Exp. Dep. Zool. [MZSP]; Dourados, Colonia Vicentina, I.1962, 4 workers, F. R. MUELLER [MZSP]; Corumbá, Serra do Urucum, 04.XII.1960, 1 gyne, K. LENKO [MZSP]; Alto do Céu, 08 km N of Fazenda Buriti, Chapada dos Guimarães, 30.XI.1986, 1 worker, C. R. F. BRANDÃO & F. H. CAETANO [MZSP]. Bahia: Mucurí, Fazenda Anfígia, 29.X.1979, 1 gyne, FORBES [CPCC]; same locality, Fazenda Boca Aberta, 17.IX.1979, 2 workers, 1 soldier, FORBES [CPCC]; Santo Amaro, ESOMI, 13.IX.1988, 3 soldiers, E. FERRAZ [CPCC]. Espírito Santo: Afonso Claudio, 1 worker, O. CONDE [MZSP]; Pedro Canário, Conceição da Barra, X.1972, 1 gyne, M. ALVARENGA [MZSP]; Linhares, IX.1972, 1 worker, M. ALVARENGA [MZSP]. Minas Gerais: Pedra Azul, 800 m, XI.1972, 1 worker, SEABRA & ALVARENGA [MZSP]. Rio de Janeiro: Porto das Caixas, Jun. 1928, 1 worker, 2 soldiers, 4 gynes, CONDE [MZSP]. São Paulo: Ilha dos Alcatrazes, 1 worker, 2 gynes, LUEDERWALDT [MZSP, NHMB]; M. Aprazível, Fazenda Bacuri, 07.VII.1974, 2 workers, 1 soldier, in *Croton* sp., J. M. DINIZ [MZSP]; Boracéia, Município Itapuí, VII.1960, 3 workers, R. MUELLER [MZSP]; Piracicaba, 31.X.1906, 1 worker, J. LIMA [MZSP]; Anhembi, Fazenda B. Rico, 14.II.1969, 1 worker, J. C. MAGALHÃES et al. [MZSP]; same locality, 21.IV.1972, 1 worker, L. TRAVASSOS [MZSP]; Adolfo, near Areia-Tietê, 21.V.1972, 3 workers, J. M. DINIZ [MZSP]; Teodoro Sampaio, XI.1973, 1 worker, F. M. OLIVEIRA [MZSP]; Boa Esperança do Sul, 26.I.1964, 1 gyne, K. LENKO [MZSP]; Agudos, III.1953, 11.X.1953, 20.XI.1955, 5 workers, 3 soldiers, W. W. KEMPF [MZSP]; VII-VIII.1958, same locality, 5 workers, R. MÜLLER [MZSP]; same locality, 28.I.1954, 1 worker, G. GILBERT [MZSP]. Paraná: Arapongas, 26.VII.1955, 2 workers,

W. W. KEMPF [MZSP]; Rolândia, 01–15.XI.1951, 6 workers, 3 soldiers, 2 gynes, W. W. KEMPF [MZSP]; Rondon, 34°36' B, 54°07' L, 500 m, 1 worker, 3 soldiers, F. PLAUMANN [MZSP]; Foz do Iguaçu, VII.1964, 1 worker, KRAUSS [USNM].

Peru: no further locality, 1 gyne [MCZC]; no further locality, 16.V.1961, intercepted in Miami, Florida, on orchids, 2 workers, 6 soldiers, 5 males [USNM]; Valle Chanchamayo, 900 m, 01.I.1959, 2 workers, WEYRAUCH [MZSP].

Bolivia: Abuna, 6 workers, 1 soldier, 1 gyne, W. M. WHEELER [MCZC, USNM]. Beni: Huachi, 1921–22, 3 workers, W. M. MANN [MZSP]. La Paz: Mapiri, 1 worker, WM. M. WHEELER [MCZC].

Argentina: Salta: Río Blanco, 20.I.1948, A. WILINK [MZSP]. Misiones: Est. Esp. Loreto, 1 worker, 1 soldier, A. A. OGLOBIN [MZSP].

Paraguay: no further locality, 1 worker, BALZAN [MCSN]. Asunción: San Bernardino, 2 workers, K. FIEBRIG [ZSMC]; Asunción, VII.1961, 1 worker, N. L. H. KRAUSS [USNM].

Discussion. - The workers and soldiers from Mexico, Guatemala, Honduras, Nicaragua and Costa Rica (in part) are larger and with denser foveae on the head than the southern representatives of the species. This geographic trend does not affect the Costa Rican specimens from Alajuela, Orotina, Turrialba and Hamburg Farm.

The subspecies *magdalenensis* (FOREL) has been described on a single black worker with sparse foveae on the head. We examined additional Colombian material similar to *magdalenensis* in colour but with and without sparse foveae on the head.

The subspecies *nanus* (FOREL) from Trinidad is equally based on a single worker with cephalic foveae denser than in *magdalenensis* and sparser than those of the specimens from the northern distributional range. Specimens from Guyana, Brazil and Venezuela are extremely similar to *nanus* in body size and sculpture. The workers from Alajuela (Costa Rica) are similar to *nanus* but the soldiers, presumably from the same nest series, are more similar to those from the northern part of the range.

The soldiers from Estación Loreto, Argentina, and from Rolândia, Paraná, have the pronotum unarmed and narrow instead of armed and with small membranaceous expansions, and the disc is narrower posteriorly instead of parallel as in all the other specimens examined. A unique worker from Salta, Argentina, has the same size as *nanus* but the foveae as in the Central American specimens.

In our cladogram, *maculatus* appears as the outgroup of all the other members of the *pinelii* clade. It is interesting to notice that the soldiers and gynes of *maculatus* are approaching but not matching the condition typical of the sister clade *pallens* for two characters at least: the frontal carinae hiding large part of the mandibles and the head and pronotum unicolour.

FERNÁNDEZ et al. (1996) report this species from the Colombian states of Huila and Valle.

Distribution: Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Trinidad, Guyanas, Brazil, Ecuador, Peru, Bolivia, Argentina, Paraguay.

Cephalotes nilpiei DE ANDRADE new species

Figs. 169, 170

Paracryptocerus pinelii (GUÉRIN) KEMPF, 1952: 26. Worker. Partim. Nec GUÉRIN, 1845. Misidentification.

Holotype: worker, Brazil, Rio de Janeiro, Parque Nacional de Itatiaia, 15.XII.1966, 950–1000 m, H. Reichardt [MZSP].

P a r a t y p e s : 9 workers and 2 soldiers, same data as the holotype (MZSP).

D e r i v a t i o n o m i n i s : *nilpiei* is an anagram of *pinelii*, the name of the species with which the new species had been previously confused.

D i a g n o s i s . - A member of the *pinelii* clade differing from its two closest ingroup species, *pileini* and *pinelii*, in the worker, by the propodeal suture more impressed, and, from *pileini*, in the soldier, by the propodeum with a pair of teeth, and from *pinelii*, in the soldier, by the shallower foveae on the head.

W o r k e r (Fig. 169). - Head subquadrate with convex frons. Frontal carinae covering the mandibles proximally and upturned in front of the eyes; border of the frontal carinae strongly crenulate anteriorly and superficially crenulate laterally. Vertexal angles broad and round, with a thin margin converging before the middle of the vertexal border. Vertexal border medially concave. Mandibles with thick lateral carina.

Mesosoma gently convex. Scapular angles absent or not visible in dorsal view. Pronotum anteriorly convex in dorsal view; pronotal sides with a membranaceous expansion anteriorly obtuse or round and narrowing posteriorly. Promesonotal suture, in dorsal view, superficially impressed. Mesonotum with a pair of thin, pointed, membranaceous teeth. Propodeal suture deeply impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous propodeal faces with a membranaceous lateral expansion originating from the propodeal suture.

Anterior face of the petiole medially slightly concave; dorsal face gently convex. Sides of the petiole with a wing-shaped, membranaceous expansion with round tip and directed laterally. Postpetiole convex dorsally; postpetiolar sides with a broad wing-shaped, membranaceous expansion with truncate tip.

Gaster suboval. First gastral tergite anterolaterally with a broad membranaceous expansion.

Legs. Mid and hind femora dorsally angulate and with a thin carina on the distal part of their dorsum. Mid and hind basitarsi compressed at the base.

Sculpture. Head dorsum reticulate, with dense, superficial, irregular foveae diminishing in size anteriorly. Frontal carinae reticulate and with sparse, shallow foveae. Ventral face of the head reticulate, with superficial, sparse foveae superimposed by thin, longitudinal rugosities more impressed on the sides. Mesosoma and pedicel with the same sculpture as on the head dorsum but the rugosities more impressed and regular on the pronotum and mesonotum. Declivous face of the propodeum reticulate and superficially rugulose. Gaster and legs reticulate. Pleurae reticulate and with longitudinal rugosities on the propleurae and anterior half of the mesopleurae.

Pilosity. Each fovea with an appressed, thick hair; similar hairs but not originating from the foveae on the membranaceous expansions, on the gaster and on the legs. External part of the frontal carinae, dorsum of the first gastral segments and posterior border of the remaining gastral segments with erect, clubbed hairs, longer on the posterior border and rare on the dorsum. Posterior border of the gastral sternites with few, long, thin, pointed hairs.

Colour. Dark brown with lighter tibiae and distal parts of the femora. Frontal carinae orange and semi-transparent. Membranaceous expansions of the body yellowish and semi-transparent. First gastral tergite anterolaterally with an orange strip surpassing the first gastral stigma, in some specimens the strip prolonged posteriorly but less pigmented. Sides of the pronotum, propodeum and pedicel with a thin, orange strip.

Measurements (in mm) and indices: TL 4.04–4.64; HL 1.00–1.16; HW 1.16–1.32; EL 0.24–0.28; PW 1.00–1.16; PeW 0.58–0.63; PpW 0.60–0.63; HBaL 0.36–0.38; HBaW 0.13–0.14; CI 113.8–116.0; PI 113.8–116.0; PPeI 172.4–184.1; PPpI 166.7–184.1; HBaI 36.1–36.8.

S o l d i e r (Fig. 170). - Head disc subquadrate, with differentiated border, raised and with crenulations more impressed anteriorly. Sides of the disc not covering completely the eyes and broadening anteriorly. Floor of the disc concave and little convex in the middle. Vertexal angles subrounded, completely separate from the disc and with superficially crenulate border. Mandibles laterally carinate and laterally hidden by the frontal carinae.

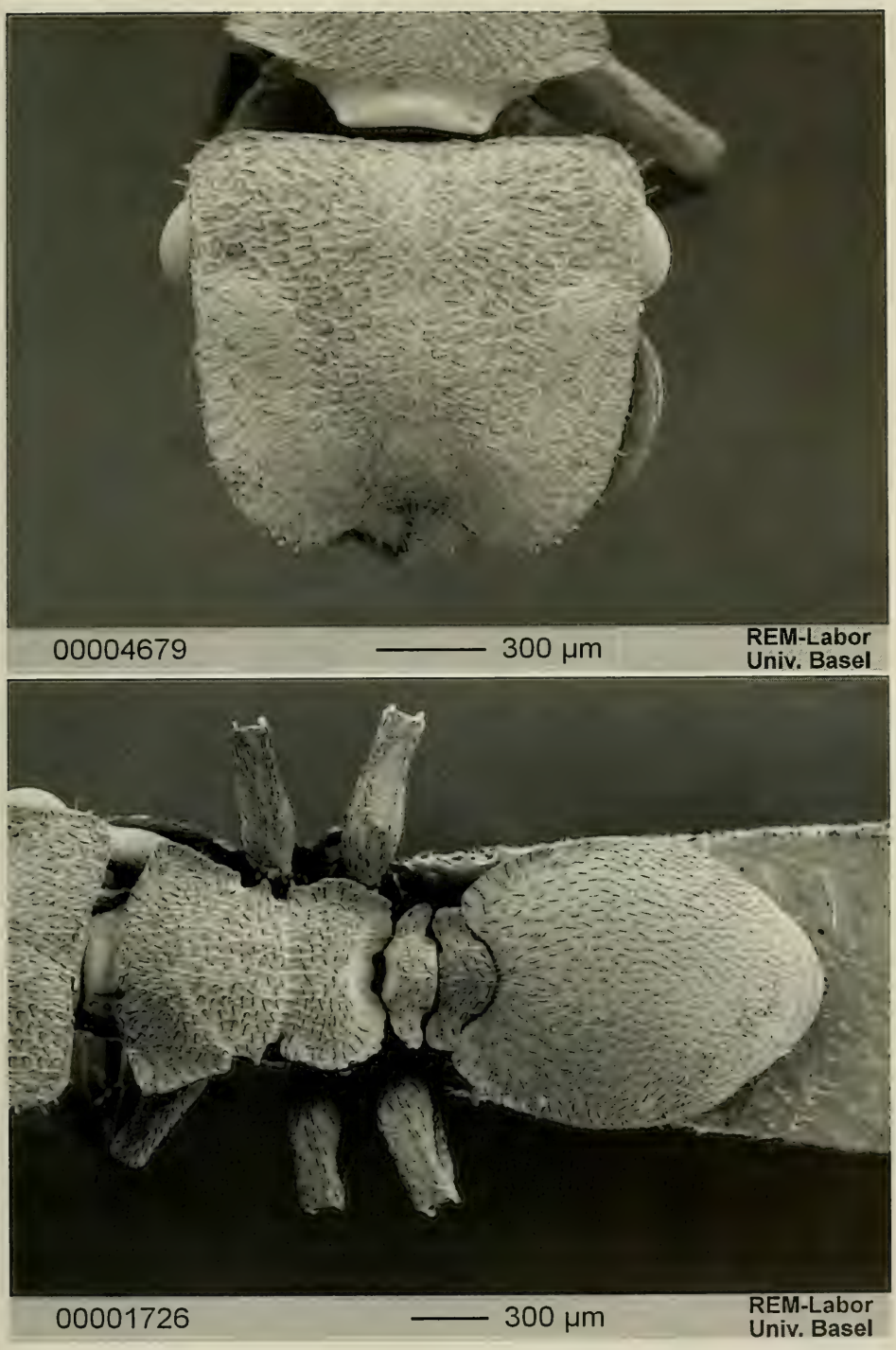


Fig. 169. *Cephalotes nilpiei* DE ANDRADE. Worker from Parque Nacional de Itatiaia, Rio de Janeiro: head (top) and meso- and metasoma (bottom) in dorsal view.

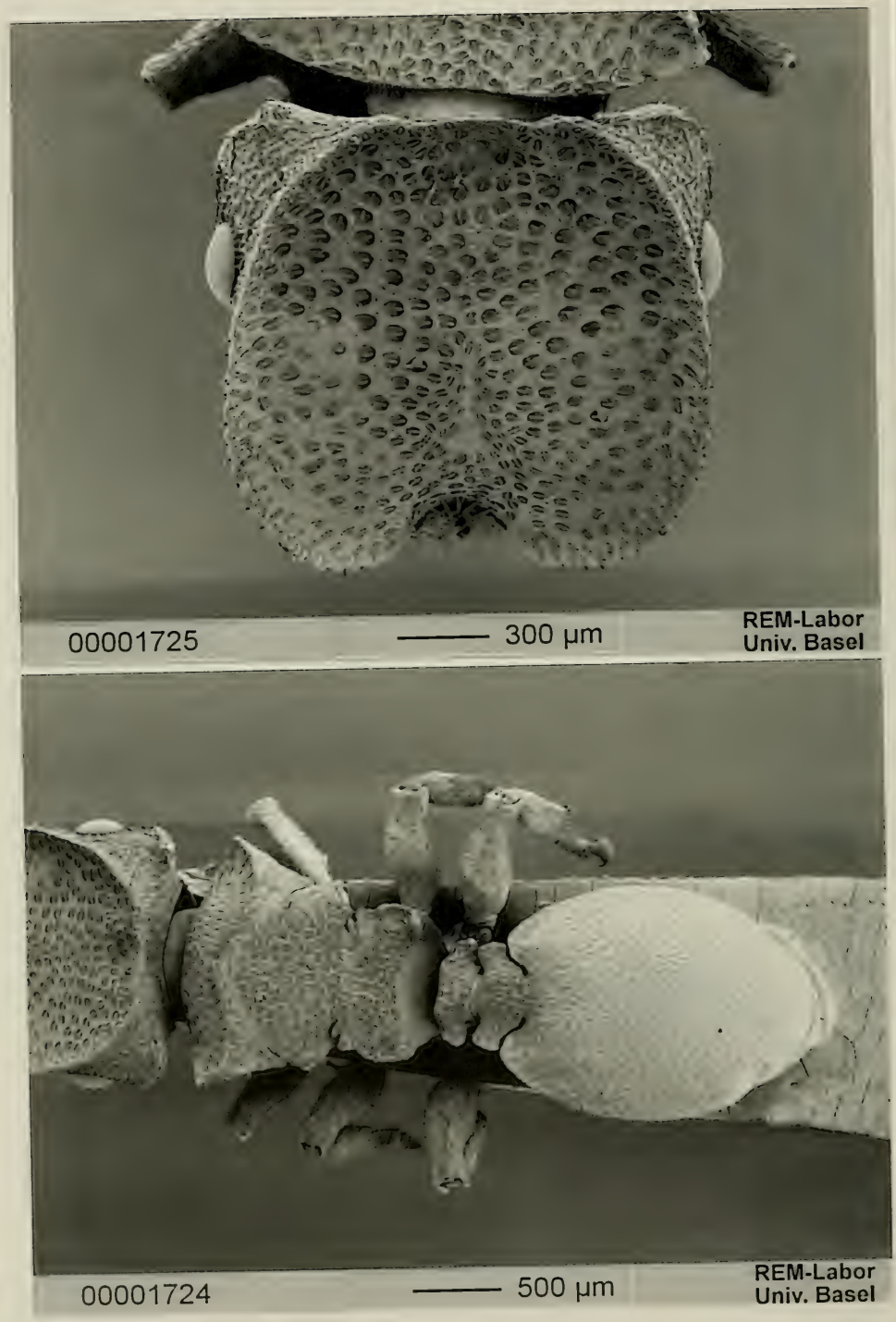


Fig. 170. *Cephalotes nilpici* DE ANDRADE. Soldier from Parque Nacional de Itatiaia, Rio de Janeiro: head (top) and meso- and metasoma (bottom) in dorsal view.

Mesosoma. Anterior pronotal border convex. Humeral angles with an obtuse, lateral, membranaceous expansion converging posteriorly up to the middle of the pronotum where it continues into the pronotal carina. Pronotal carina high, separate in the middle by an incision, each half posteriorly convex and diminishing in height towards the middle of the pronotum. Posterior half of the pronotal sides strongly converging posteriorly. Pronotal suture impressed in dorsal view. Promesonotal suture deeply impressed. Mesonotal sides with a pair of broad, obtuse teeth followed by a pair of vestigial, thin, minute denticles. Propodeum with differentiate basal and declivous faces; sides of the basal face forming cranially a pair of obtuse expansions directed anteriorly and followed by a convex, narrow, membranaceous expansion converging posteriorly into a pair of denticles curved upwards. Declivous face of the propodeum narrowing posteriorly and with a broad, membranaceous expansion.

Pedicel, legs and gaster as in the worker but with the membranaceous expansions less broad.

Sculpture. Head dorsum superficially reticulate, slightly shining and with foveae; the foveae contiguous posteriorly diminishing in size and more superficial anteriorly. Ventral face of the head reticulate and with thin, longitudinal rugosities; the two anterior thirds of the ventral face of the head with superficial, irregular foveae. Mesosoma reticulate and with dense foveae, smaller and irregular on the basal face of the propodeum. Pedicel with the same sculpture as the mesosoma but with smaller and shallower foveae. Declivous face of the propodeum, gaster and legs reticulate. Pleurae reticulate and with longitudinal rugosities on the propleurae only.

Pilosity. As in the worker but with the clubbed hairs also on the mesosoma.

Colour. Black with lighter tibiae and distal part of the femora. Frontal carinae orange and semi-transparent. Membranaceous expansions of the body yellowish and semi-transparent. First gastral tergite anterolaterally with an orange spot surpassing the first gastral stigma posteriorly, another spot but lighter before the posterior border. Sides of the pronotum, propodeum and pedicel with an orange strip.

Measurements (in mm) and indices: TL 5.40–5.68; HL 1.36–1.40; HW 1.48; EL 0.30–0.31; PW 1.40–1.48; PeW 0.61–0.63; PpW 0.62–0.64; HBaL 0.40–0.42; HBaW 0.15–0.16; CI 105.7–108.8; PI 100.0–105.7; PPeI 222.2–242.6; PPpI 218.7–238.7; HBaI 37.5–38.1.

Material examined. - **Brazil**: Rio de Janeiro: Parque Nacional de Itatiaia, 15.XII.1966, 950–1000 m, 10 workers, 2 soldiers (type series), H. Reichardt [MZSP]; Itatiaia, VII.1954, 1 worker, Barth [MZSP]; Petrópolis, 14.XII.1944, 15.VI.1945, 7 workers, W. W. Kempf [MZSP]; same locality, 1 worker, T. Borgmeier [MCZC].

Discussion. - *C. nilpiei* is very similar to *pinelii*. Kempf (1952) already noticed that the workers from Petrópolis he studied, differ from the true *pinelii*, but, having no soldiers associated with them, he preferred not to separate them as a distinct species. We have been able to examine additional workers from Rio de Janeiro associated with soldiers and identical with those examined by Kempf (1952). The workers of *nilpiei* differ from those of true *pinelii* by the shallower foveae and superficial longitudinal rugosities, by the pronotum generally narrower (see the PW and PI values), by the membranaceous expansions of the postpetiole broader and by the propodeal suture impressed. The soldiers of *nilpiei* differ from those of *pinelii* by the head disc with sparser foveae, by the shallower groove on the vertex and by the narrower propodeum.

Distribution: Brazil.

Cephalotes pileini de Andrade new species

Figs. 171, 172

Cryptocerus pinelii (Guérin) Emery, 1905, nec Guérin, 1845. Soldier and gyne. Misidentification.

H o l o t y p e : soldier, Argentina, Córdoba, La Carlota, SILVESTRI [MCZC].

P a r a t y p e s : four workers and one gyne [MCZC], one worker and one gyne [MCSN], one worker and one soldier [MZSP], three workers and one soldier [NHMB], same data as the holotype.

D e r i v a t i o n o m i n i s : *pileini* is an anagram of *pinelii*, the name of the species with which this species had been previously confused.

D i a g n o s i s . - A member of the *pinelii* clade differing from its outgroup species, *nilpiei*, and from its ingroup species *pinelii*, in the worker, by the head longer than the pronotal width, and, from the soldier of *nilpiei* and *pinelii*, by the floor of the disc less concave and by the absence of propodeal teeth.

W o r k e r (Fig. 171). - Head subquadrate with convex frons. Frontal carinae covering the mandibles proximally and slightly upturned above the eyes Vertexal angles round, with a thin, membranaceous margin converging and narrowing before the middle of the vertexal border. Mandibles with thick lateral carina.

Mesosoma gently convex. Scapular angles absent or not visible in dorsal view. Anterior border of the pronotum convex in dorsal view; pronotal sides with a membranaceous expansion anteriorly obtuse and narrowing posteriorly. Promesonotal suture, in dorsal view, superficially impressed on the sides only. Mesonotum with a pair of pointed or obtuse, membranaceous teeth. Propodeal suture impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous propodeal faces with a membranaceous lateral expansion originating from the propodeal suture.

Anterior face of the petiole medially concave; dorsal face gently convex. Sides of the petiole with a wing-shaped, membranaceous expansion with round tip and directed laterally. Postpetiole convex dorsally; postpetiolar sides also with a wing-shaped, membranaceous expansion with round tip.

Gaster oval and elongate. First gastral tergite anterolaterally with a broad membranaceous expansion.

Legs. Mid and hind femora dorsally angulate and with a carina on the distal part of their dorsum. Mid and hind basitarsi compressed at the base.

Sculpture. Head dorsum minutely reticulate, with dense foveae diminishing in size anteriorly. Ventral face of the head reticulate and with superficial, dense foveae forming longitudinal rugosities anteriorly. Mesosoma and pedicel reticulate, with irregular, dense foveae forming longitudinal, irregular rugosities, the foveae smaller on the propodeum and on the pedicel. Gaster and legs deeply reticulate. First gastral tergite with thin, longitudinal rugosities on the anterior third, the rugosities becoming thinner and more superficial posteriorly. Membranaceous expansions of mesosoma, pedicel and gaster reticulate, the latter with few, thin, longitudinal rugosities anteriorly.

Pilosity. Each fovea with an appressed hair; similar hairs but not originating from the foveae and slightly thinner on the membranaceous expansions, on the gaster and on the legs. Posterior border of the gastral segments with rare, erect, clubbed hairs.

Colour. Dark brown with lighter legs. Frontal carinae orange and semi-transparent. Membranaceous expansions of the body yellowish and semi-transparent. First gastral tergite anterolaterally with an orange, long, thin strip directed posteriorly. Some specimens with the head darker than the rest of the body.

Measurements (in mm) and indices: TL 3.55–4.44; HL 0.86–0.96; HW 0.93–1.06; EL 0.24–0.25; PW 0.79–0.89; PeW 0.54–0.61; PpW 0.53–0.63; HBaL 0.25; HBaW 0.10; CI 108.1–110.4; PI 117.7–117.8; PPeI 146.3–147.5; PPpI 142.8–149.0; HBaI 40.0.

S o l d i e r (Fig. 172). - Head disc subround, with differentiated border and raised more on the sides than posteriorly. Sides of the disc not covering completely the eyes and broadening anteriorly. Floor of the disc concave and with a small tumulus in the middle. Vertex with a superficial depression.

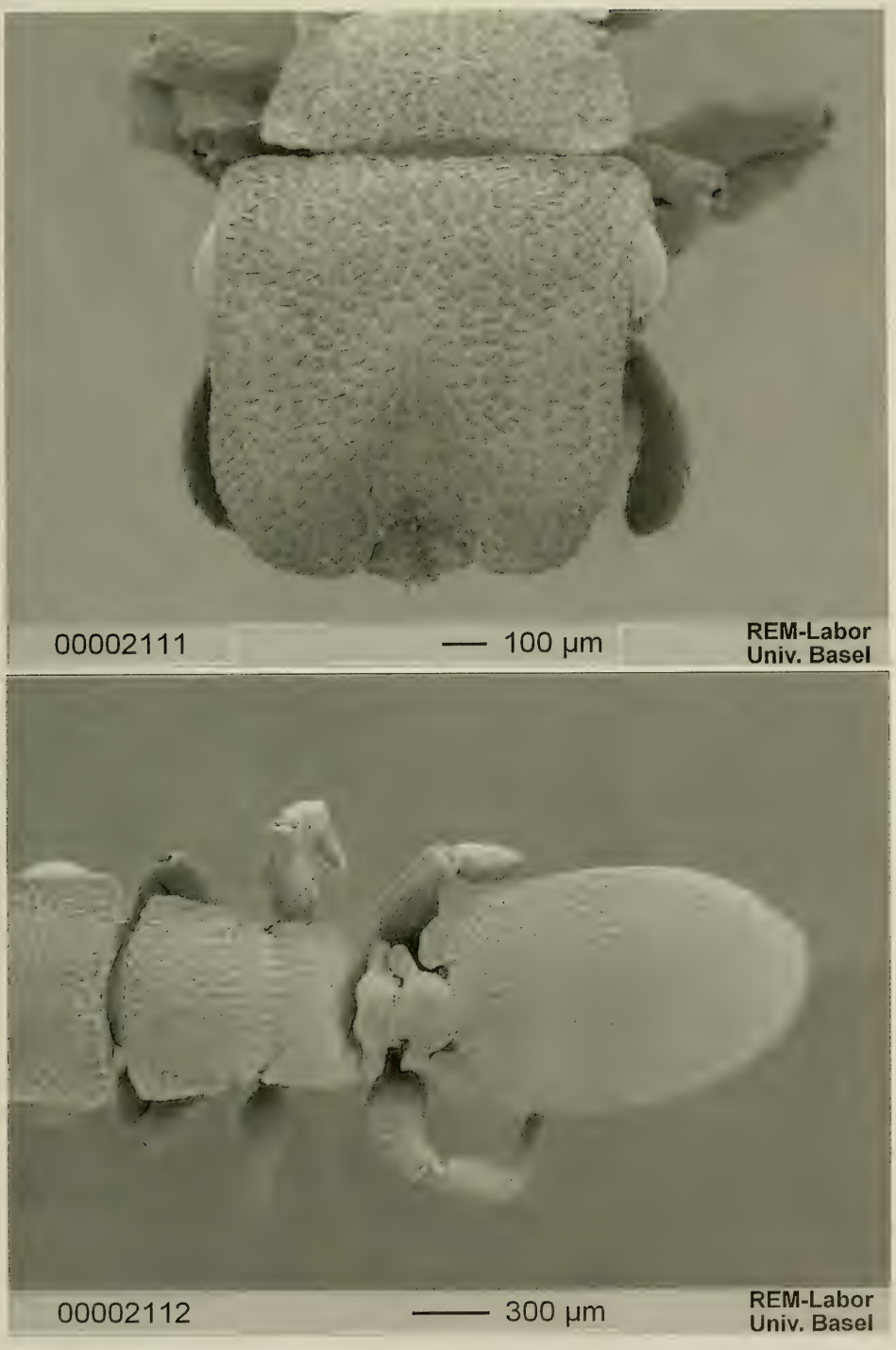


Fig. 171. *Cephalotes pileini* DE ANDRADE. Worker from Córdoba, Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

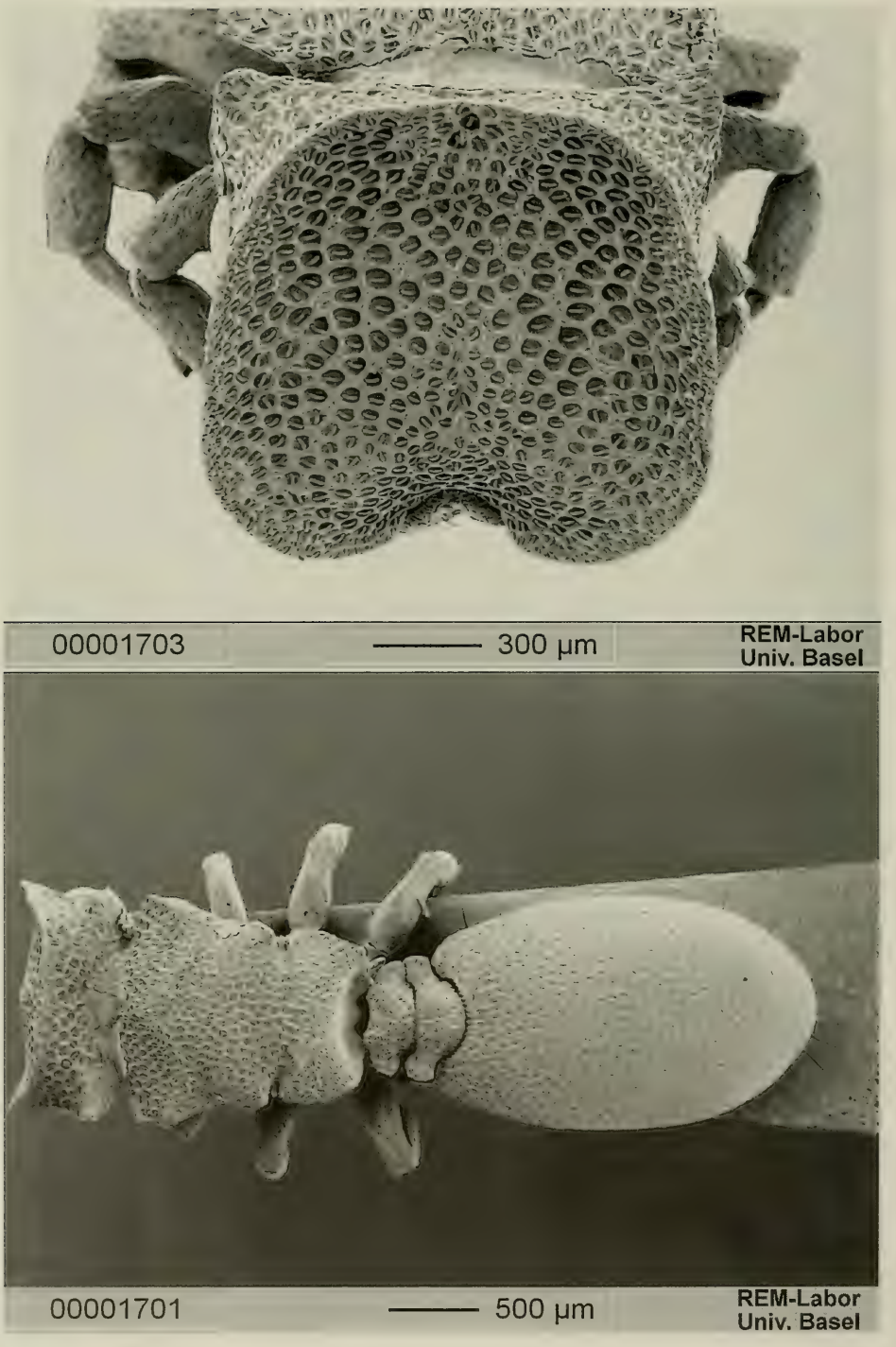


Fig. 172. *Cephalotes pileini* DE ANDRADE. Soldier from Córdoba, Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

Vertexal angles round, completely separate from the disc and with superficially crenulate border. Mandibles laterally carinate and laterally hidden by the frontal carinae.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a narrow, obtuse, lateral, membranaceous expansion converging posteriorly up to the middle of the pronotum where it continues into the poorly marked pronotal carina. Posterior half of the pronotal sides strongly converging posteriorly. Pronotal suture in dorsal view impressed on the sides. Promesonotal suture deeply impressed. Mesonotal sides with two pairs of teeth, the anterior pair broad, and with truncate tips, the posterior pair small, thin and pointed. Propodeum with differentiate basal and declivous faces; sides of the basal face convex, with the posterior half bearing a narrow membranaceous expansion extending and broadening up to the end of the declivous face.

Pedicel as in the worker but with the expansions less broad.

Legs as in the worker but with the dorsal carina less impressed.

Gaster oval, with a margin not reaching the stigma posteriorly.

Sculpture. Head dorsum, mesosoma and pedicel reticulate-punctate and covered by dense foveae, smaller and shallower on the border of the disc and on the clypeus, on the propodeum and on the pedicel. Ventral face of the head reticulate and with irregular, superficial foveae and irregular rugosities. Declivous face of the propodeum reticulate and with thin, longitudinal rugae. Gaster and legs strongly reticulate and with superficial, minute foveae. First gastral tergite with thin, longitudinal rugosities on the anterior third, less impressed and irregular posteriorly.

Pilosity. Each fovea with an appressed hair. Legs and gaster with appressed hairs thinner and shorter than those originating from the foveae. Border of the disc over the eyes, and posterior border of the gastral segments with rare clubbed hairs. The sternites bear, in addition a few long, thin, slightly pointed hairs.

Colour. Dark brown with the sides of the mesonotum, of the pedicel and of the first gastral tergite with a lighter strip.

Measurements (in mm) and indices: TL 5.14–5.40; HL 1.20–1.26; HW 1.32–1.36; EL 0.25–0.28; PW 1.28–1.32; PeW 0.64–0.65; PpW 0.67–0.69; HBaL 0.27; HBaW 0.12; CI 107.9–110.0; PI 103.0–103.1; PPeI 200.0–203.1; PPpI 185.5–197.0; HBaI 44.4.

G y n e . - Head disc present. Head dorsum gently convex posteriorly and with concave anterolateral sides. Frontal carinae superficially crenulate, expanded anteriorly, converging posteriorly and connected by a convex carina on the vertex. Vertex between the pair ocelli with a superficial depression. Vertexal angles round and with marked margin. Eyes visible in full dorsal view. Ocelli remote from the posterior border of the head disc. Anterior clypeal border deeply concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border gently convex. Humeral angles obtuse. Pronotal sides straight. Pronotal carina absent. Promesonotal suture impressed. Lower mesopleurae with a denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face convex; declivous face converging posteriorly and with a narrow membranaceous border on the posterior half.

Petiolar sides convex and with marked margin. Postpetiolar sides with a round lobe directed anteriorly.

Gaster with a pair of broad, anteriorly protruding lobes.

Sculpture. Head dorsum reticulate and with dense foveae diminishing in size anteriorly and less impressed in the middle of the frontal carinae. Mesosoma and pedicel with the same type of sculpture as on the anterior part of the head dorsum, but with sparser foveae on the middle of the mesonotum. Declivous face of the propodeum, gaster and legs as in the soldier.

Pilosity. As in the soldier.

Colour. Brown, floor of the disc darker. Frontal carinae orange and semi-transparent. Sides of the pronotum and of the propodeum yellowish. First gastral tergite with two pairs of yellowish spots, the first pair anterolateral and the second one before the posterior border.

Measurements (in mm) and indices: TL 6.72–7.00; HL 1.26–1.32; HW 1.26–1.28; EL 0.31–0.32; PW 1.24; PeW 0.58; PpW 0.69–0.72; HBaL 0.40; HBaW 0.14; CI 97.0–100.0; PI 101.6–103.2; PPeI 213.8; PPpI 172.2–179.7; HBaI 35.0.

Material examined. - **Argentina**: Córdoba: La Carlota, 9 workers, 3 soldiers and 2 gynes, SILVESTRI (type series) [MCZC, MCSN, MZSP, NHMB].

Discussion. - *C. pileini* is very similar to *pinelii*. EMERY (1905) already noted that soldiers and a unique gyne referable to the species described here as *pileini* were different from those of true *pinelii*, but preferred not to describe them. We had the opportunity to re-examine probably all what remains of the material collected by SILVESTRI and scattered in different collections by EMERY. All the Argentinean workers from La Carlota and described here as *pileini* differ from those of *pinelii* (known only from Paraguay and Brazil) by the head and gaster much longer, by the membranaceous expansions of the mesosoma narrower, and by the foveae much denser and irregular. The soldiers and gynes of *pileini* differ from those of *pinelii* by the vertexal groove shallower, by the border of the frontal carinae less crenulate, by the hairs on the frontal carinae sparser, by the foveae less impressed and by the pronotal crest very reduced in the soldier and absent in the gyne.

Distribution: Argentina.

Cephalotes pinelii (GUÉRIN-MÉNEVILLE) new combination
Figs. 173, 174, 175, 176, 177, 178

Cryptocerus pinelii GUÉRIN-MÉNEVILLE, 1845: 425. Worker. Original description. Type locality: Morro Queimado (Rio de Janeiro, Brazil). Type material: presumably lost (EMERY, 1894 a), not found in the ZSMC.

Cryptocerus pinelii GUÉRIN, EMERY, 1890: 75, pl. 9, fig. 10. Worker, soldier and gyne.

Cryptocerus grandinosus (SMITH), FOREL, 1908: 354. Nec SMITH, 1860. Misidentification.

Paracryptocerus pinelii (GUÉRIN), KEMPF, 1952: 22, figs. 6, 10, 15. Worker, soldier, gyne, male (not described). First combination in *Paracryptocerus*.

Zacryptocerus pinelii (GUÉRIN), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *pinelii* clade differing from its two closest species, *liepini* and *pileini*, as follows: in the worker, from *liepini* by the shallower sculpture, and from *pileini*, by the head as long as the pronotal width, and in the soldier from both species by the deeper depression on the vertex.

Worker (Fig. 173) (description of KEMPF, 1952). - „Length 3.5–4.1 mm. Color variable. Brownish-black to ferruginous; callows may be ochraceous as *grandinosus*. Funiculus and legs ferruginous. Frontal carinae and membraneceous borders of the thorax, peduncle and gaster pale testaceous. In fully colored specimens the peripheral portions of the first gastral tergite are distinctly paler than the discal portions.

Head subquadrate, slightly longer than wide, longer than thorax, scarcely tapering cephalad; the interocular width greater than the median head length. Sides of head straight, scarcely upturned above eyes. Occipital corners rounded and membranaceous. Occipital border scarcely emarginate. Greatest diameter of eyes less than one fourth of maximum head length.

Thorax as long as broad across the pronotum. Shoulders rounded or obtusely angulate. Sides of thorax forming a rentrant angle at mesonotum, which has, on each side, a submembranaceous, projecting denticule. Mesoepinotal suture vestigial mesally. Epinotum narrower than pronotum, with distinct basal and declivous faces. Dorsum of hind femora longitudinally marginate distad of the angle, but without a dorsal and ventral crest.

Petiole shallowly and broadly impressed antero-mesally. Membranaceous lobes of peduncular segments less expanded than in *grandinosus*.

Gaster ovate, usually elongate, with anterolateral, rounded, membranaceous borders.

Opaque, finely shagreened. Head and thorax with squamiferous foveolae on dorsum. First gastral tergite with fine, more or less longitudinal rugulae on the basal half. Sides of thorax and the declivous face without striae. Scales shiny and appressed, smallest on gaster. No erect setae on the first gastral tergite."

Measurements (in mm) and indices: TL 3.16–4.46; HL 0.78–1.04; HW 0.90–1.18; EL 0.22–0.26; PW 0.80–1.04; PeW 0.50–0.60; PpW 0.51–0.60; HBaL 0.23–0.33; HBaW 0.09–0.11; CI 110.4–115.4; PI 110.4–113.5; PPeI 153.8–173.3; PPpI 156.9–173.3; HBaI 33.3–39.1.

S o l d i e r (Fig. 174) (description of KEMPF, 1952). - „Length 4.8–5.7 mm. Head, thorax, peduncle and appendages ferruginous, often somewhat infuscated. Gaster slightly darker, the first tergite with a broad, pale band toward the anterior border and along the sides, the disc brownish black. Membranaceous portions of frontal carinae, shoulders, epinotum and peduncular segments pale testaceous.

Head about as long as wide, surmounted by a circular, strongly excavate, disc, the border of which is crenulated. Cephalic disc with a median longitudinal convexity, and a deeply excavate groove mesally on the occipital border, flanked by strong ridges. Supramandibular excision subsemicircular. Part of the disc covering the antennal scrobe membranaceous.

Thorax shorter than head, slightly broader than long. Shoulders membranaceous, obtusely angulate. Sides of pronotum moderately convex. Transverse pronotal carina crested. Mesonotum about twice as broad as long, with a more or less rounded, projecting lobe on each side. Basal and declivous faces of epinotum narrowly crested, the posterior corners of the basal face having an upturned tubercular tooth. Femora as in worker.

Peduncular segments similar to those of worker.

Gaster elongate, the anterolateral borders evenly rounded.

Disc of head somewhat shiny, less so on dorsum of thorax. Both strongly, coarsely, and densely foveolate. Gaster with the same minute rugulae as in worker."

Measurements (in mm) and indices: TL 4.64–5.36; HL 1.16–1.36; HW 1.32–1.44; EL 0.28–0.32; PW 1.28–1.44; PeW 0.58–0.70; PpW 0.58–0.67; HBaL 0.30–0.33; HBaW 0.11–0.12; CI 94.4–113.8; PI 97.1–103.1; PPeI 205.7–222.9; PPpI 206.1–222.9; HBaI 34.4–40.0.

G y n e (Fig. 175) (description of KEMPF, 1952). - „Length 6.5–7.0 mm. Color as in soldier with the following differences: occipital lobes, shoulders, basal face of epinotum, orange-brown; disc of head, scutum, sides of thorax, and gaster infuscated. The portion of the cephalic disc covering the antennal scrobe is partly membranaceous. First gastral tergite with an elongate, yellowish macula on each corner, the pair on each side nearly fusing.

Head as in soldier, but more elongate. Cephalic disc elliptical, excavate laterad, moderately convex discally. Borders of the disc distinctly crested and submembranaceous. Median groove on vertex as in soldier.

Thorax longer than wide. Shoulders angulate. Transverse pronotal carina vestigial to obsolete. Anterior tooth of lower mesopleura small or absent. Basal face of epinotum with a blunt rounded, lateral lobe and a strong, rather blunt teeth on the posterior corner.

Petiole with a small denticule on each side, pointing obliquely caudad. Anterolateral lobes of gaster rounded.

Wings hyaline, the venation brunneous. Marginal cell of fore wing closed and appendiculate. Transverse cubital vein present.

Sculpture and pilosity as in soldier. Scales on gaster minute, appressed."

Wings as in Fig. 176.

Measurements (in mm) and indices: TL 6.36–7.36; HL 1.28–1.32; HW 1.26–1.38; EL 0.32–0.33; PW 1.24–1.36; PeW 0.54–0.61; PpW 0.70–0.76; HBaL 0.36–0.43; HBaW 0.12–0.15; CI 94.4–104.5; PI 98.4–106.4; PPeI 203.3–251.8; PPpI 168.4–214.9; HBaI 33.3–38.9.

M a l e (Fig. 177) (previously undescribed). - Head (eyes included and mandibles excluded) 1/3 broader than long; vertexal angles convex. Vertex slightly protruding dorsally and bearing salient ocelli. Compound eyes broadly convex, in the middle of the sides of the head. Frontal carinae diverging backwards, not reaching the median ocellus posteriorly. Frons flat. Clypeus slightly convex; its posterior border marked by a convex sulcus, the anterior border concave medially and laterally denticulate. Mandibles slender. Scapes thick, twice as long as

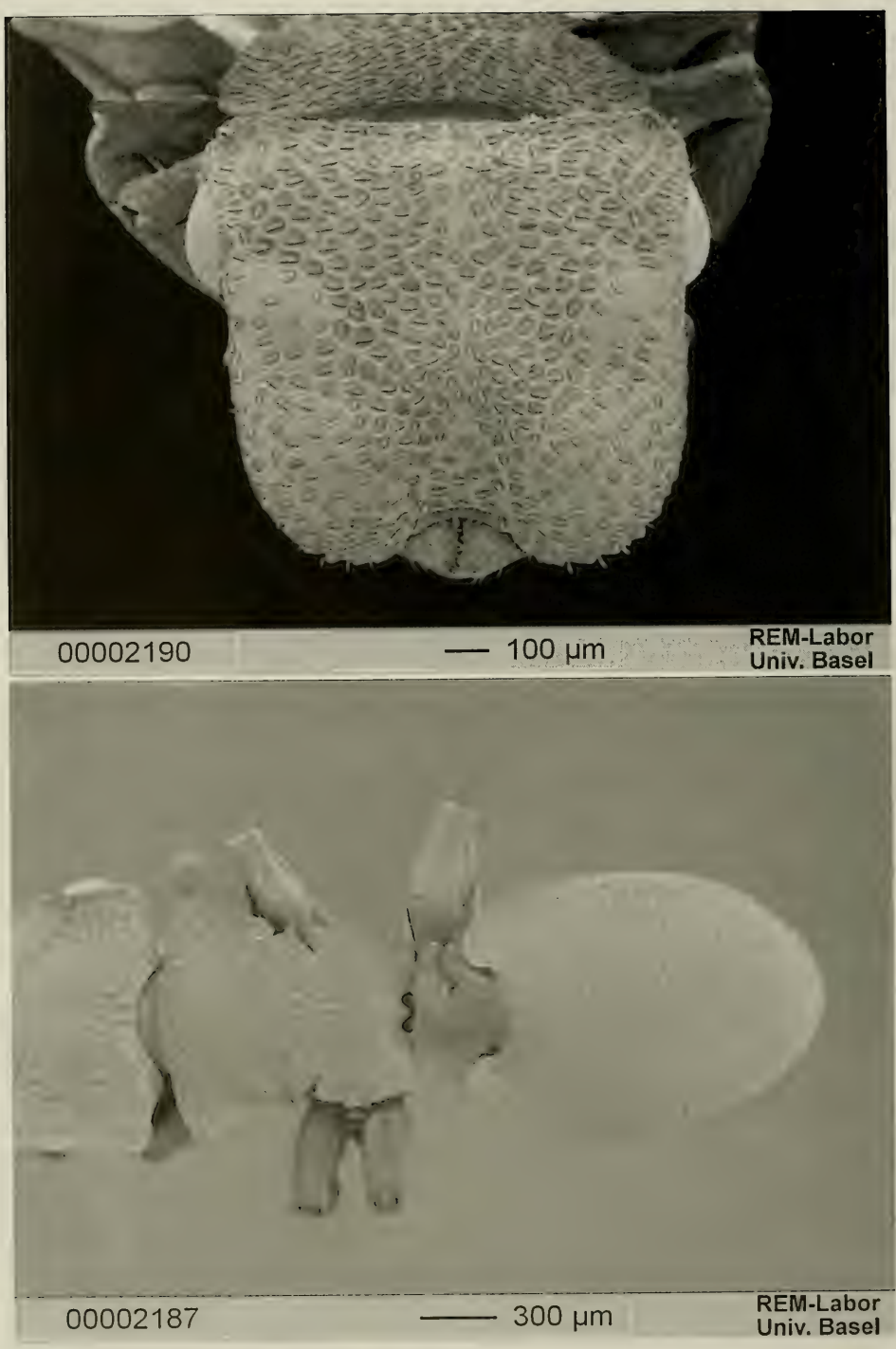


Fig. 173. *Cephalotes pinelii* (GUÉRIN-MÉNEVILLE). Worker from Serra da Caraça (Minas Gerais), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

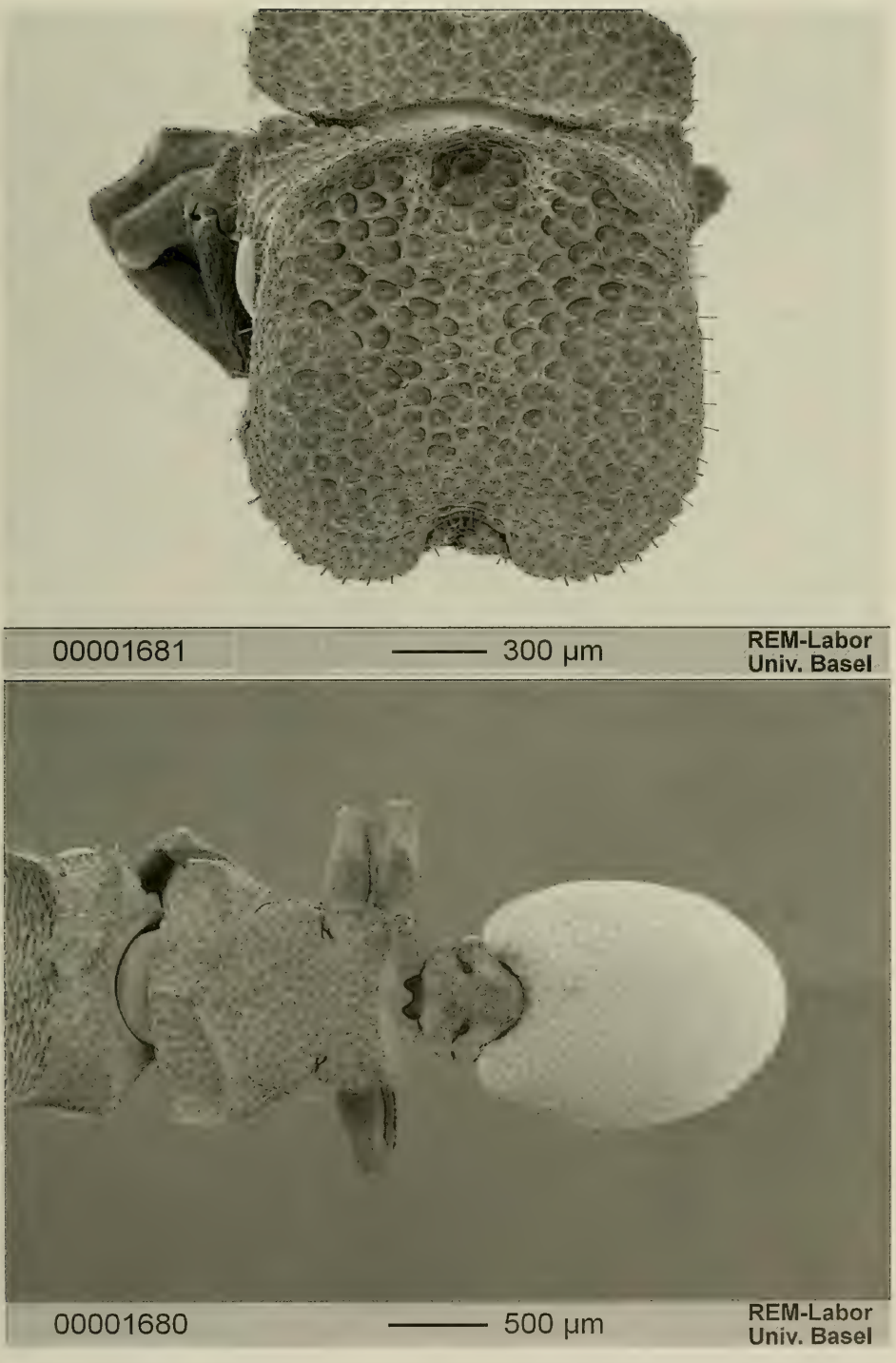


Fig. 174. *Cephalotes pinelii* (Guérin-Méneville). Soldier from Serra da Caraça (Minas Gerais), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

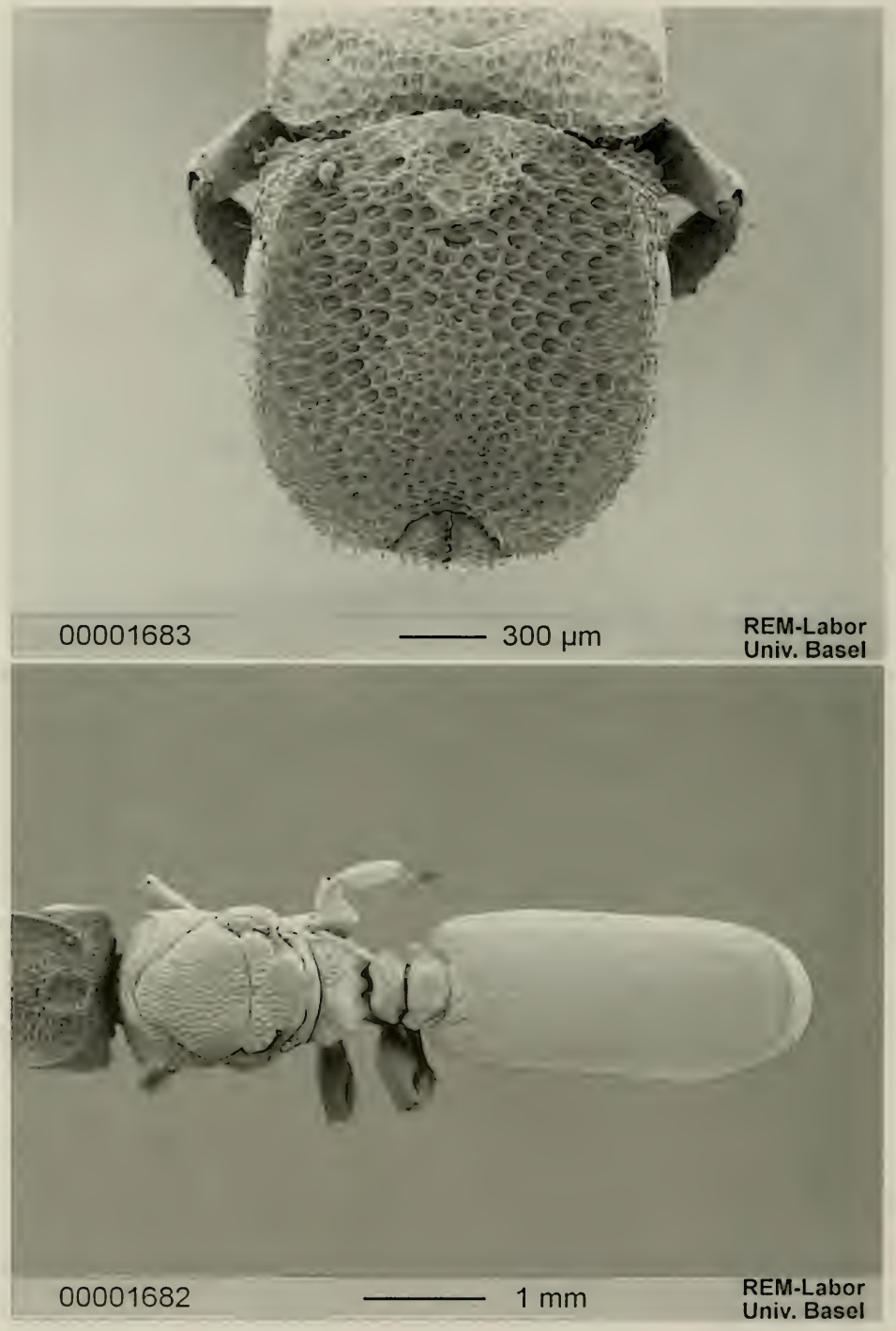


Fig. 175. *Cephalotes pinelii* (GUÉRIN-MÉNEVILLE). Gyne from Nova Teutônia (Santa Catarina), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

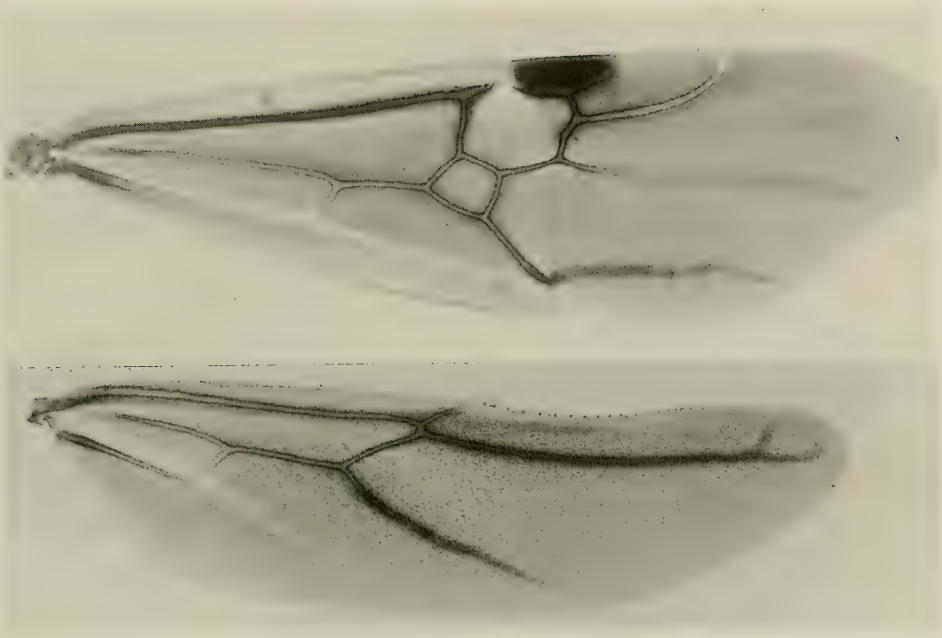


Fig. 176. *Cephalotes pinelii* (GUÉRIN-MÉNEVILLE). Gyne from Nova Teutônia (Santa Catarina), Brazil, fore and hind wings.

the first funicular joint; remaining funicular joints filiform and thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards and feebly carinate. Mesonotal scutum convex in side view; median Mayrian furrow superficially impressed and visible in some specimens only. Scutellum convex, its sides converging posteriorly. Basal and declivous faces of the propodeum differentiated; basal face unarmed and with the sides converging posteriorly; declivous face with the sides carinate and converging posteriorly.

Petiole as broad as the postpetiole; its anterior face concave. Petiolar sides convex or slightly obtuse anteriorly, converging posteriorly. Postpetiole laterally and dorsally convex.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 178.

Wings. As in the gyne.

Sculpture. Head and mesosoma reticulate-punctate, with sparse, irregular foveae and irregular rugosities, the rugosities more regular on the centre of the ventral part of the head and on the pleurae. Pedicel superficially reticulate and with faint longitudinal rugosities. Gaster and legs reticulate, the reticulation less impressed on the legs.

Pilosity. Body with three types of hairs: (1) long, thin, pointed hairs dense on the head, on the mesosoma, sparse on the pedicel; (2) shorter than the cephalic hairs, decumbent on the gaster and on the legs; (3) short, subtruncate, subdecumbent on the funiculi.

Colour. Head, mesosoma, pedicel and coxae black. Gaster, femora and tarsi castaneous-brown. Tibiae yellow to light brown.

Measurements (in mm) and indices: TL 4.52–4.86; HL 0.66–0.71; HW 0.85–0.91; EL 0.35; PW 0.84–0.91; PeW 0.42–0.47; PpW 0.40–0.46; HBaL 0.41–0.44; HBaW 0.08; CI 128.2–128.8; PI 100.0–109.0; PPeI 193.6–200.0; PPpI 197.8–210.0; HBaI 18.2–19.5.

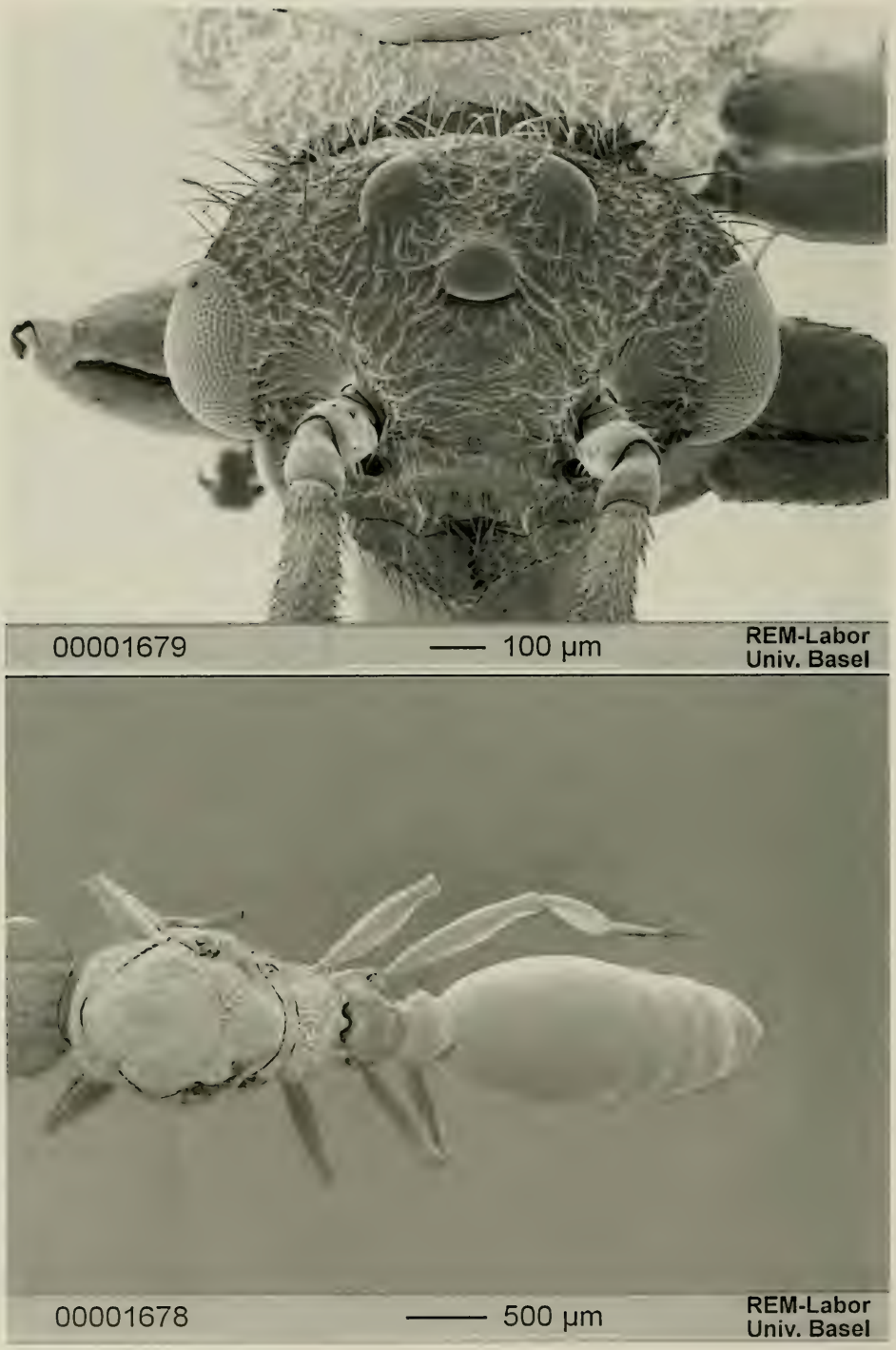


Fig. 177. *Cephalotes pinelii* (Guérin-Méneville). Male from Serra da Caraça (Minas Gerais), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

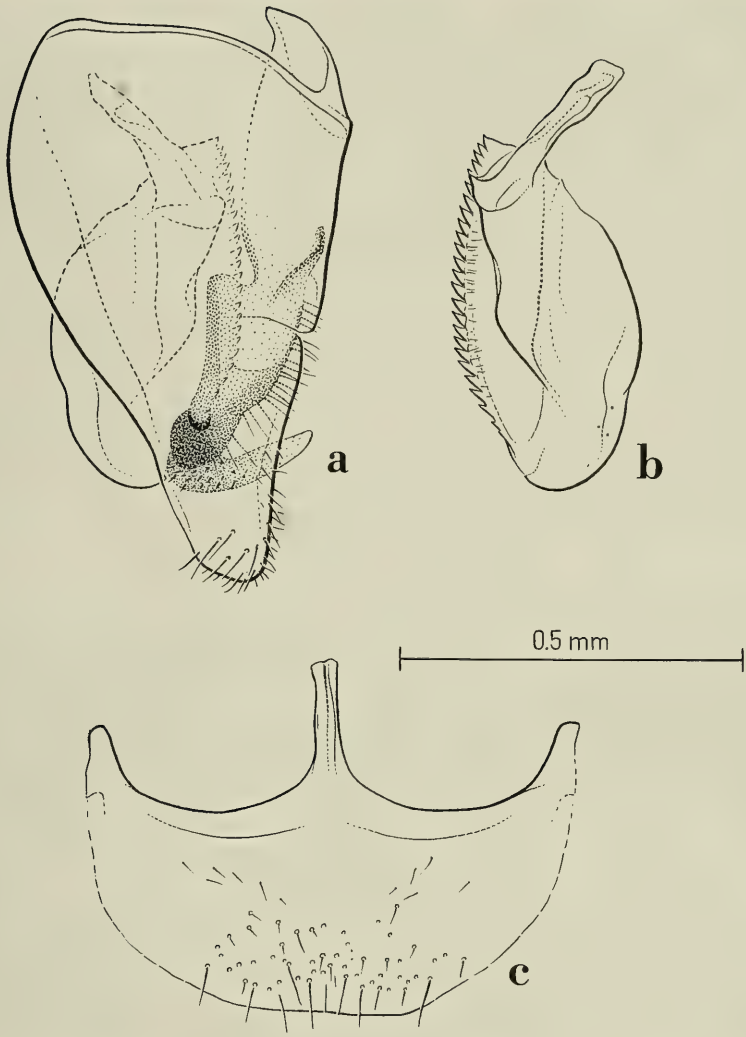


Fig. 178. *Cephalotes pinelii* (Guérin-Méneville). Male from Serra da Caraça (Minas Gerais), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Material examined. - **Brazil**: Piauí: Teresina, Sta. Teresa, 15.X.1980, 1 worker, A. J. Almeida [MZSP]. Minas Gerais: no further locality, II.1923, 3 workers, L. Lohoman [MZSP]; Serra da Caraça, XI.1961, many workers, soldiers, gynes and males, Kloss, Lenko, Martins & Silva [MZSP]; Caraça, Sta. Bárbara, III.1971, 1 worker, F. M. Oliveira; Palmira, I.1929, 1 gyne [MZSP]; São João del Rei, IX.1925, 1 worker, F. Zacharias [MZSP]. São Paulo: no further locality, 3 workers, 2 soldiers, 2 gynes, 2 males, Jhering [MHNG]; São Paulo, Butantan, 16.IX.1971, 1 worker, L. Travassos [MZSP]; São Sebastião, 06.III.1958, 11 workers, 3 gynes, W. W. Kempf [MZSP]; São Paulo, Ipiranga, 2 workers, 3 soldiers, Jhering [MHNG]; same locality, 1906–1908, 11 workers, 3 soldiers, 3 gynes, 5 males, Luederwaldt [MZSP]; same locality, 12.VI.1906, 13.VIII.1906,

08.VI.1908, 12 workers, 8 soldiers, 3 gynes, 6 males, LUEDERWALDT [MZSP]; Mauá, V.1961, 1 worker, N. L. H. KRAUSS [USNM]; Barueri, 10.VI.1958, 15 workers, 2 soldiers, K. LENKO [MZSP]; Ibiuna, V.1972, 1 worker, A. CARVALHO [MZSP]. Rio de Janeiro: Teresópolis, Colônia Alpina, 1 soldier, GÖLDI [MHNG]. Paraná: Rolândia, 25 workers, 5 soldiers, 1 gyne, W. W. KEMPF [MCZC, MZSP]; Ponta Grossa, 20.XI.1994, 1 worker, B. H. DIETZ [MZSP]; Curitiba, 04–05.II.1969, 1 worker, PORTER & GARCÍA [MCZC]; same locality, 1 worker, 15.I.1964, C. VALLE [MZSP]; same locality, III.1954, 1 worker, N. L. H. KRAUSS [USNM]. Santa Catarina: Imbicarem, IX.1960, 1 worker, F. PLAUMANN [MZSP]; Pareci Novo, 11.VIII.1926, 11 workers, 1 soldier, S. J. RAMBO [MZSP]; Florianópolis, I.1958, 5 workers, R. MUELLER [MZSP]; Nova Teutônia, X.1971, XI.1972, 3 workers, 2 soldiers, 1 gyne, F. PLAUMANN [MZSP]; same locality, 27°14' B, 52°23' L, IX.1936, VII & VIII.1959, VI.1960, I & XI.1963, XII.1974, VI.1975, IV.1976, 23 workers, 7 soldiers, 6 gynes, F. PLAUMANN [MZSP]; same locality, 13.IX.1935, 1 worker [NHMB]; Blumenau, 12.X.1921, 1 worker, M. WITTE [MZSP]; Chapecó, XII.1957, 1 worker, F. PLAUMANN [MZSP]; Rio das Antas, I.1953, 1 gyne, CAMARGO [MZSP]. Rio Grande do Sul: no further locality, 11 workers, 5 soldiers, 1 gyne, JHERING [MHNG, MCSN]; no further locality, 09.VI.1908, 2 workers, JHERING [MZSP]; no further locality, VII.1969, 12 workers, 3 soldiers, R. L. ARAÚJO [MZSP]; Barros Cassal, 700 m, IX.1969, 1 worker, F. PLAUMANN [MZSP]; Porto Alegre, 25.VII.1930, 1 worker, 1 soldier, S. J. BUCK [MZSP]; Pelotas, 23.VII.1965, 1 worker, Exp. Dep. Zool. [MZSP].

Paraguay: Alto Paraná: Pastoreo, 09.XII.1974, 2 workers, P. DUELLI [MZSP].

Discussion. - *C. pinelii* is easily recognisable among the other species of the clade by the deep vertexal depression of the soldier and of the gyne. The worker could be confused with that of *pileini* but it differs from it by the much longer gaster. The workers from the southernmost parts of the distribution of this species (Rio Grande do Sul and Paraguay) are lighter (i. e. brownish) than those of the remaining parts of its area (black). The gyne from S. Paulo tentatively described as *grandinosus* by FOREL (1908) is a dwarf specimen but otherwise typical *pinelii* in all its characters.

Distribution: Brazil and Paraguay.

Cephalotes liepini DE ANDRADE new species
Figs. 179, 180

Holotype: worker, Brazil, Goiás, Alvorada do Norte, Fazenda Mattos, 08–12.VII.1991, C. R. F. BRANDÃO [MZSP].

Paratypes: 7 workers, 1 soldier, same data as the holotype (MZSP).

Derivatio nominis: *liepini* is an anagram of *pinelii*, the name of a close species.

Diagnosis. - A member of the *pinelii* clade characterised in the worker by the membranaceous expansions of the gaster bent dorsally and in the soldier by the following combination of characters: large, deep, irregular and contiguous disc foveae bearing an erect, clubbed hair, petiole and postpetiole with round expansions, and vertex only superficially depressed.

Worker (Fig. 179). - Head subquadrate; frons convex. Frontal carinae covering the mandibular sides and slightly upturned above the eyes. Vertexal angles obtuse, with a thin, membranaceous margin converging and narrowing before the middle of the vertexal border. Mandibles with thick lateral carina.

Mesosoma gently convex. Scapular angles absent or not visible in dorsal view. Anterior border of the pronotum gently convex in dorsal view; pronotal sides with a membranaceous expansion anteriorly obtuse and narrowing posteriorly. Promesonotal suture impressed. Mesonotum with a small pair of triangular, membranaceous teeth. Propodeal suture impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous propodeal faces with a membranaceous lateral expansion starting from the propodeal.

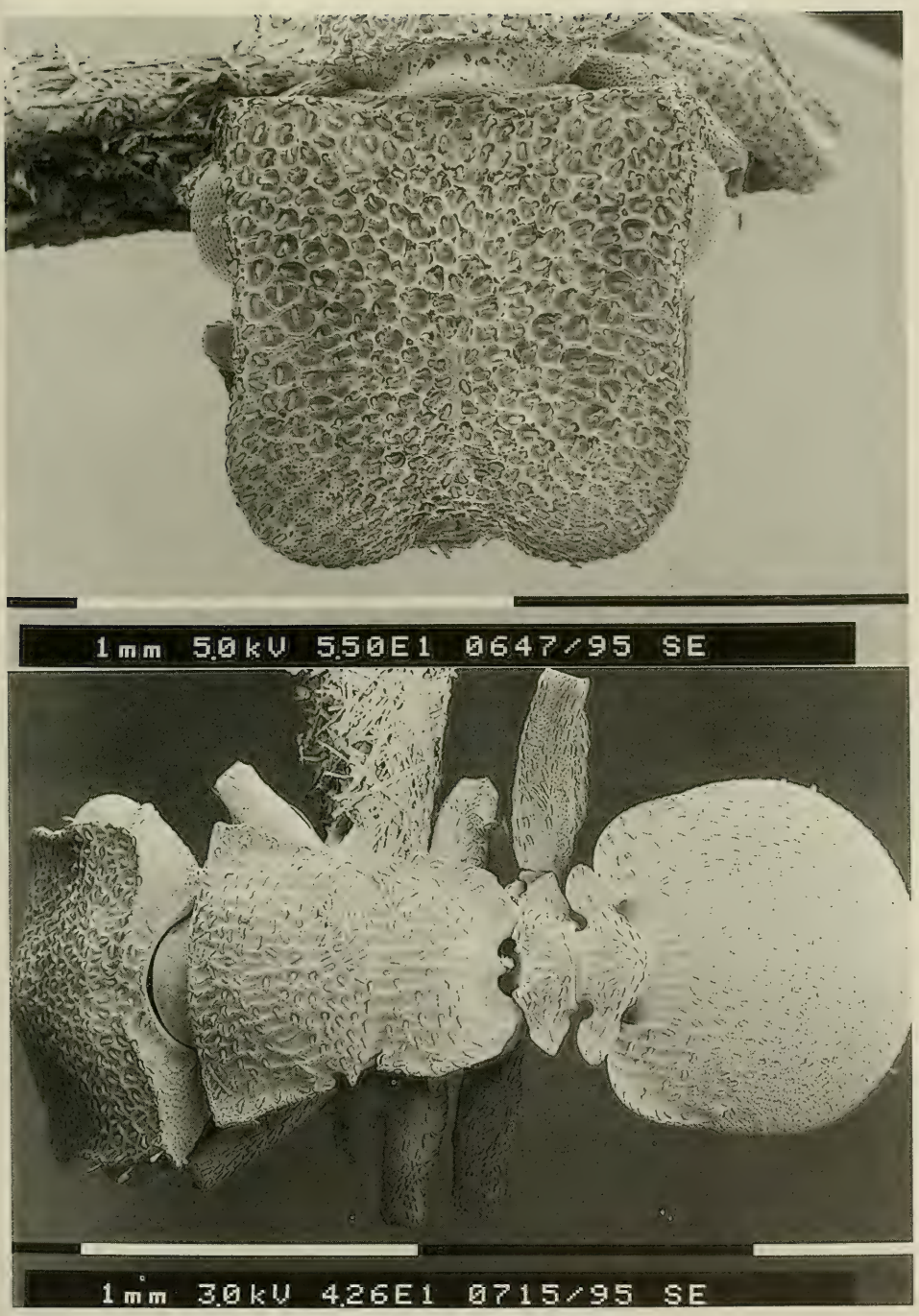


Fig. 179. *Cephalotes liepini* DE ANDRADE. Worker from Alvorada do Norte (Goiás), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Petiole with a concave anterior face bearing a pair of denticles; postpetiolar dorsum sloping anteriorly. Sides of the petiole with a wing-shaped, membranaceous expansion with pointed or round tip. Postpetiole convex dorsally; postpetiolar sides with another broad, wing-shaped, membranaceous expansion with round tip.

Gaster oval. First gastral tergite anterolaterally with a broad membranaceous expansion.

Legs. Mid and hind femora dorsally angulate and with a faint carina on the distal part of their dorsum. Mid and hind basitarsi compressed at the base.

Sculpture. Head dorsum with dense foveae smaller on the anterior fourth. Ventral face of the head reticulate with superficial, dense foveae forming longitudinal rugosities on the anterior part only. Mesosoma and pedicel reticulate-punctate. Mesonotum with irregular, dense foveae, the foveae separated by longitudinal, irregular rugosities on the propodeum only. Pedicel with small, dense foveae. Gaster and legs deeply reticulate and with superficial, small foveae. Thin, longitudinal rugosities on the anterior third of the first gastral tergite. Membranaceous expansions of mesosoma, pedicel and gaster reticulate and with few, thin, longitudinal rugosities.

Pilosity. Each fovea with a decumbent, canaliculate hair; similar hairs but not originating from the foveae on the membranaceous expansions. Hairs on the gaster and on the legs appressed and thinner than those on head and mesosoma. Frontal carinae over the eyes and posterior part of the gastral segments with rare to sparse, erect, clubbed hairs. The sternites bear, in addition rare long, thin, erect, slightly pointed hairs.

Colour. Brown. Frontal carinae orange and semi-transparent. Membranaceous borders of the body yellowish and semi-transparent. Tarsi brown. First gastral tergite anterolaterally with an orange, thin strip almost reaching the end of the tergite.

Measurements (in mm) and indices: TL 3.40–4.08; HL 0.84–0.96; HW 0.92–1.08; EL 0.24–0.28; PW 0.74–0.92; PeW 0.44–0.56; PpW 0.48–0.60; HBaL 0.23–0.28; HBaW 0.09–0.11; CI 109.5–112.5; PI 117.4–124.3; PPeI 164.3–168.6; PPpI 153.3–159.2; HBaI 39.1–39.3.

S o l d i e r (Fig. 180). - Head disc subquadrate, with the border differentiated, irregularly crenulate, raised more on the sides then posteriorly. Sides of the disc not covering completely the eyes and broadening anteriorly. Floor of the disc concave laterally and gently convex in the middle. Vertexal angles obtuse, completely separate from the disc and with marked, irregularly crenulate border. Mandibles laterally carinate and laterally hidden by the frontal carinae.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a small, obtuse, lateral membranaceous expansion converging posteriorly up to the middle of the pronotum where it continues into the pronotal carina. Posterior half of the pronotal sides strongly converging posteriorly. Pronotal carina higher on the sides than medially, each half gently convex posteriorly. Pronotal suture impressed. Promesonotal suture deeply impressed. Mesonotal sides with a pair of broad, round expansion followed by a pair of minute, pointed denticles. Propodeum with differentiate basal and declivous faces; sides of the basal face with a narrow, crenulate border, the border forming anteriorly a small pair of obtuse teeth directed anteriorly, the rest converging posteriorly. Declivous face of the propodeum with the sides narrowing posteriorly and with a small, membranaceous lateral expansion.

Pedicel as in the worker but with the expansions less broad.

Legs as in the worker but with the dorsal carina less impressed.

Gaster oval, with a narrow, membranaceous expansion not reaching the stigma posteriorly.

Sculpture. Head dorsum, mesosoma and pedicel superficially punctate and covered by large, dense foveae, smaller on the border of the disc, on the clypeus and on the pedicel. Ventral face of the head reticulate and with sparse, superficial foveae and few, thin, irregular rugosities laterally. Declivous face of the propodeum superficially reticulate and with longitudinal, thin rugae. Gaster and legs strongly reticulate and with superficial small foveae.

Pilosity. Each fovea of the head dorsum with an erect hair; each fovea of the mesosoma with a subdecumbent hair; each fovea of the pedicel, of the gaster and of the legs with a decumbent or an appressed hair. Frontal carinae, vertexal angles, mesosoma, posterior border of the gastral tergites and sternites with rare to sparse clubbed hairs. The sternites bear, in addition a few long, thin, slightly pointed hairs.

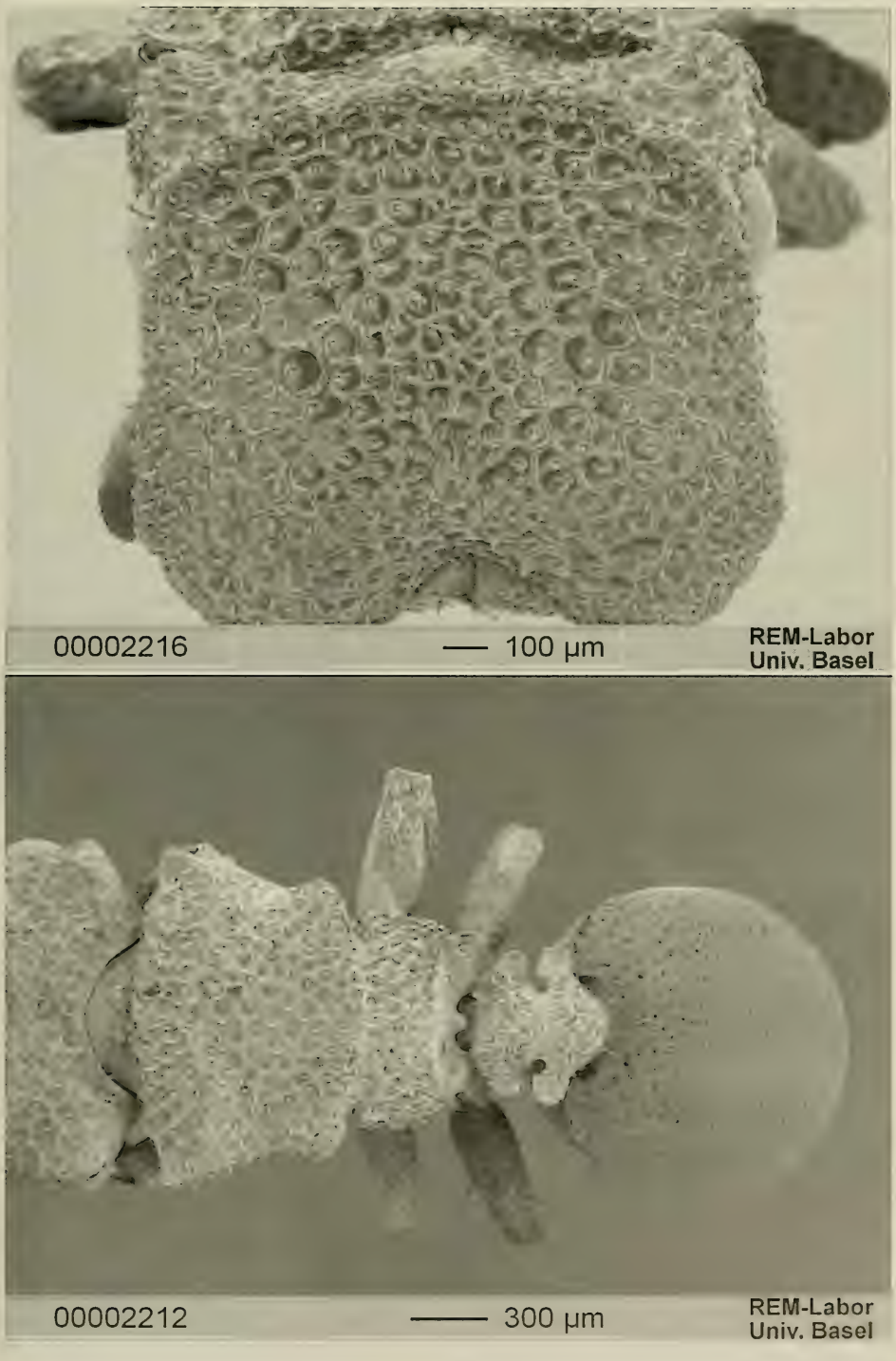


Fig. 180. *Cephalotes liepini* DE ANDRADE. Soldier from Alvorada do Norte (Goiás), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Colour. As in the worker but with the frontal carinae darker. First gastral tergite with the second third dark brown.

Measurements (in mm) and indices: TL 4.80; HL 1.12; HW 1.32; EL 0.28; PW 1.32; PeW 0.56; PpW 0.60; HBaL 0.30; HBaW 0.12; CI 117.86; PI 100.0; PPeI 235.7; PPpI 220.0; HBaI 40.0.

Material examined. - **Brazil**: Goiás: Alvorada do Norte, Fazenda Mattos, 08–12.VII.1991, 8 workers (holotype and paratypes), 1 soldier (paratype), C. R. F. BRANDÃO [MZSP].

Discussion. - The worker and the soldier of *liepini* are easily characterised from the other species of the clade as stated in the diagnosis. The soldier of *liepini* shares with *kukulcan* the disc foveae with an erect or suberect, clubbed hair and the humeri with narrow, membranaceous expansions and a narrow pronotal crest. The worker of *liepini* is unique within the *pinelii* clade for sharing with some species of the *grandinosus* clade the membranaceous expansions of the gaster bent dorsally, but *liepini* differs, however, from all the species of the *grandinosus* clade by the absence of crest on the mid and hind femora, a synapomorphic character of the latter clade.

Distribution: Brazil.

Cephalotes kukulcan SNELLING new species

Figs. 181, 182, 183, 184, 185

?*Zacryptocerus scutulatus*, LONGINO & COLWELL, 1996: fig. (without number). Worker. Probable misidentification deduced from our examination of the figure.

Type material: holotype soldier from Belize, Stann Creek District, Twin Cays, 16 Jan. 1987, J. F. LYNCH (LACM); paratypes (all Belize and all collected by J. F. LYNCH): 2 gynes, 12 soldiers and 22 workers, same data as the holotype; 3 soldiers and 3 workers, 3 males, Man-O-War Cay, 3 June 1985; 1 gyne, 1 worker, 1 male, Ragged Cay, 25 June 1985; 2 soldiers and 7 workers, „Jellyfish Cay", Blue Ground Range, 31 May 1985; 4 soldiers and 8 workers, „Beetle Cay", Blue Ground Range, 31 May 1985; 1 gyne, 2 soldiers and 18 workers, North Grand Bogue Cay, Turneffe Atoll, 29 March 1993. Paratypes in BMNH, LACM, MCZC, and USNM.

Derivatio nominis: This species is named for Kukulcan, the Mayan equivalent to the „Feathered Serpent", Quetzalcoatl, of the Aztecs. The name is a noun in apposition.

Diagnosis. - A member of the *pinelii* clade superficially similar to other species from which it differs as follows: from *scutulatus*, in the worker, by the frontal carinae weakly upturned above the eyes and, in the soldier and gyne, by the dense, deep, irregular and contiguous foveae on the disc; from *liepini*, in the worker and soldier, by the pointed petiolar and postpetiolar spines.

Worker (Fig. 181) (description of R. R. SNELLING, personal communication). - „Measurements (mm): HW (greatest head width below the eyes) 0.83 - 0.95, HL (greatest length from the lower margin of the frontal lobes to the highest level of the margin of the vertex) 0.94–1.03, TL 3.2–3.7.

Head about 1.10 (1.07–1.13) times as long as broad; lateral margins very weakly divergent above, dorsolateral corners weakly crested; vertexal margin thin, cariniform and weakly concave in frontal view. Front of head gently convex; disc dull and very shallowly reticulate-foveate, each fovea with appressed, glittering scale-like seta. Side of head densely covered with appressed, glittering, scale-like hairs. Gular area dull, contiguously micropunctate and with scattered foveae, each with appressed scale-like seta.

Mesosoma. Anterior margin of pronotal disc without humeral angle; lateral margin with narrow lamelliform crest that is irregular but not denticulate; side of mesonotum with short,

acute tooth; propodeum with irregular lateral crest continuous to petiolar insertion; entire dorsum reticulate-foveate, foveae larger and more distinct than those of frons and each with appressed, scale-like glittering seta. Side of mesosoma dull and finely granulopunctate; mesepisternum and side of propodeum with appressed, glittering scale-like setae on lower one-half or more. Legs as in soldier.

Petiole and postpetiole about as in soldier but spines less robust.

Metasomal tergum 1 invaginated at postpetiolar insertion; anterolateral corner narrowly marginate and slightly reflexed; disc granulose and dull, with dense appressed, glittering scale-like setae and sparse, short, erect, stout setae scattered across preapical margin; disc with scattered fine appressed hairs.

Color. Frontal lobes, mesosomal lamellae, spines of petiole and postpetiole, and large anterolateral spots of metasomal tergum 1 translucent yellowish; legs variably dull yellowish to reddish; remainder of body dark reddish brown to blackish."

Measurements (in mm) and indices: TL 3.24–4.05; HL 0.80–1.00; HW 0.84–1.08; EL 0.21–0.30; PW 0.72–0.95; PeW 0.48–0.56; PpW 0.56–0.71; HBaL 0.28–0.32; HBaW 0.07–0.08; CI 105.0–108.3; PI 113.0–116.7; PPeI 150.0–167.3; PPpI 128.6–146.0; HBaI 25.0–25.8.

S o l d i e r (Fig. 182) (description of R. R. SNELLING, personal communication). - „Measurements (mm): holotype HW ((greatest head width below the eyes)) 1.41, HL (greatest length from the lower margin of the frontal lobes to the highest level of the margin of the vertex) 1.60, TL 5.4. Paratypes: HW 1.24–1.41; HL 1.28–1.51; TL 4.3–5.1.

Head with complete frontal shield, about 1.10 (1.03–1.14) times as long as wide; margins of shield strongly elevated, straight or weakly concave across middle one-third of vertex margin; dorsolateral corners of head fully visible in frontal view, thin and elevated, margins irregular; disc anteriorly distinctly sloping towards clypeus, center of disc slightly convex; entire disc, from rim to rim, sharply and coarsely reticulate-foveate, each fovea with erect, short, capitate or pyriform seta; rim with appressed, spatulate setae internally and with erect capitate to spatulate setae externally. Side of head and vertex coarsely reticulose and with subappressed, scale-like glittering setae. Gular area slightly shiny, irregularly more or less longitudinally rugulose with some reticulate laterad and scattered fine, setose foveae.

Mesosoma. Transverse pronotal carina distinct, narrowly interrupted in middle, its dorsal margin irregular; lateral margin with one or two short denticulae anteriorly, posteriorly confluent with transverse carina; disc reticulate-foveate, each fovea with appressed, glittering scale-like seta. Mesoscutum with short, blunt lateral lobe; sculpture similar to pronotum, but reticulae finer. Basal face of propodeum similar to sculpture of mesonotum, laterally without spines or teeth, but posterolateral angle prominent; side of declivity narrowly lamellate; disc of declivity without striae, shallowly and contiguously punctate. Side of mesosoma dull, contiguously micropunctate, with scattered irregular rugules, lower mesepisternum and side of propodeum with setiferous foveae, setae appressed, glittering and scale-like. Procoxa, in profile, without basal coniform process. Dorsal margin of profemur subangulate at about midlength; meso- and metafemora angulate at midlength of dorsal face, all femora beyond middle with appressed, glittering scale-like setae.

Petiole with declivitous anterior face; lateral spines stout, flattened and slightly curved caudad; postpetiolar spines slightly stouter and longer; dorsal faces of both segments dull, with appressed, glittering, scale-like setae.

Metasoma elongate, tergum 1 about 1.2 times as long as wide; tergum 1 dull, granulopunctate and with well separated appressed, glittering, scale-like setae that become sparser and narrower toward posterior margin. Disc of sternum 1 shiny and weakly sculptured, becoming minutely and contiguously punctate at extreme sides.

Color. Frontal shield and dorsum of pronotum largely dull reddish, usually with dark brownish above mandibles; some reddish color often also present on side of mesonotum and propodeum base; legs variable, tibiae and tarsi always light to dark reddish, often legs almost entirely reddish; gaster varying reddish and blackish, but tergum 1 yellow marked with prominent anterolateral spot, sometimes with anterior and posterior marks confluent so that tergum 1 is largely pale but with large dark median stripe that is broadest anteriorly."

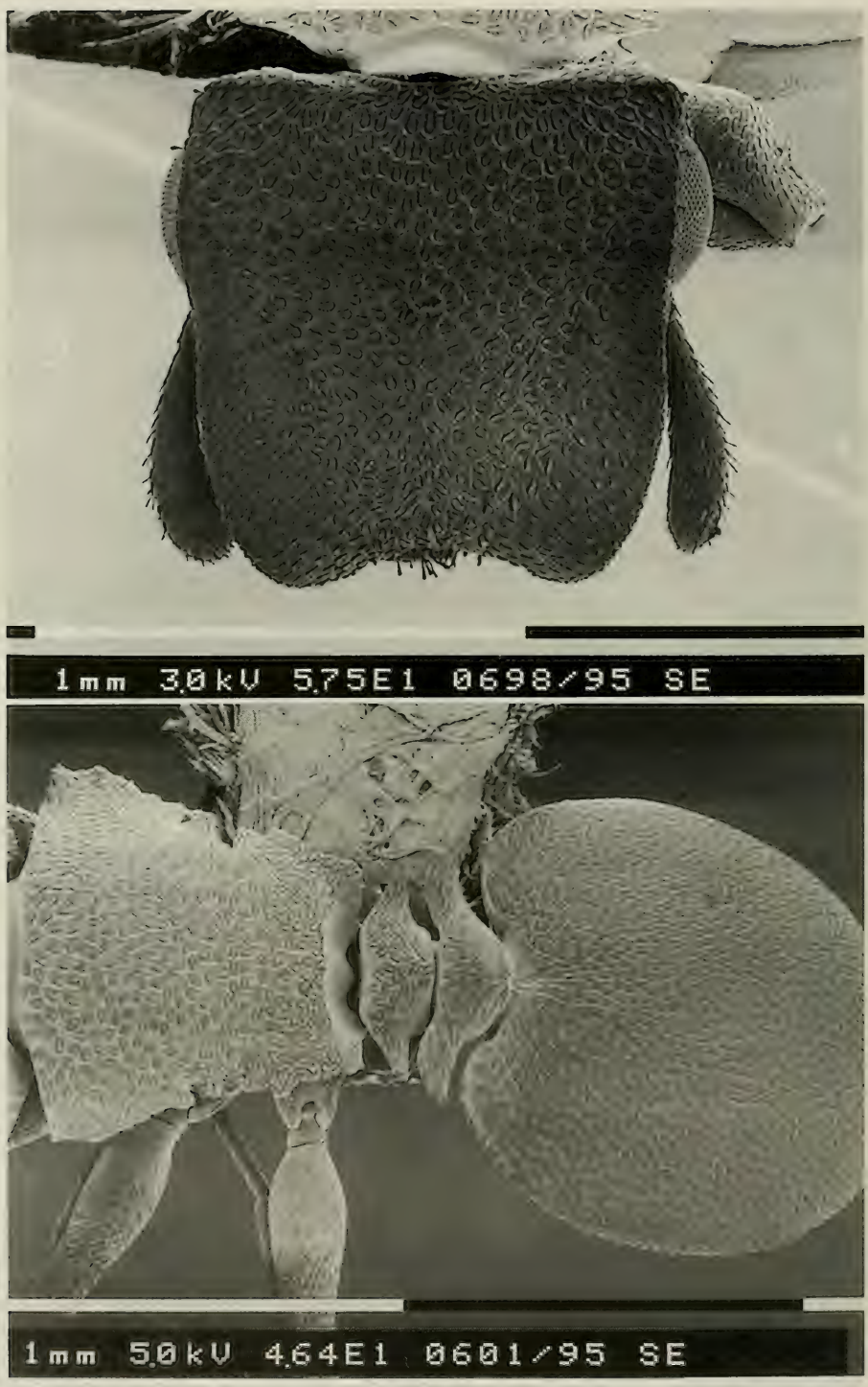


Fig. 181. *Cephalotes kukulcan* SNELLING. Worker from Man-O-War Kay, Belize: head (top) and meso- and metasoma (bottom) in dorsal view.

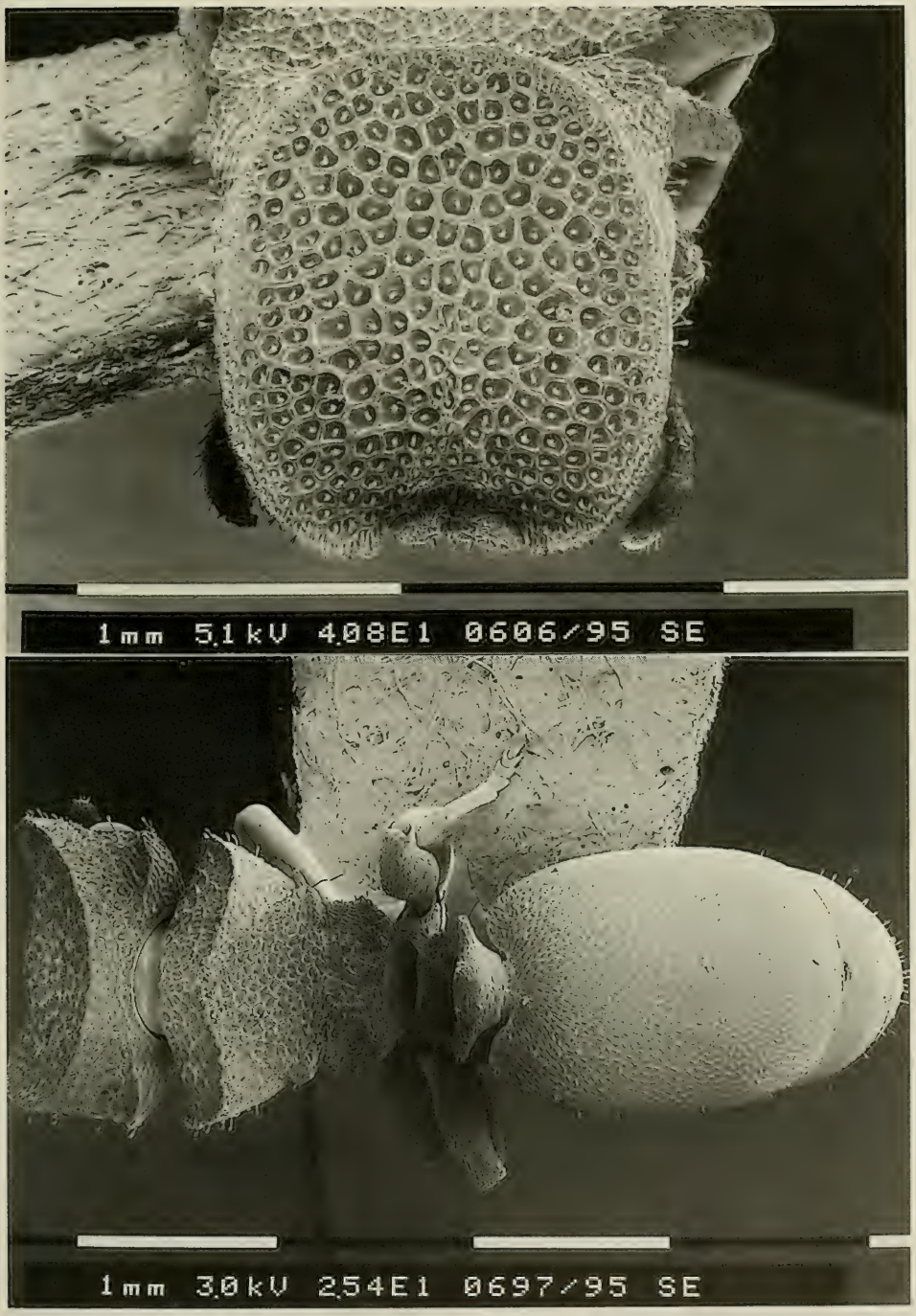


Fig. 182. *Cephalotes kukulcan* SNELLING. Soldier from Man-O-War Kay, Belize: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 4.48–5.60; HL 1.16–1.44; HW 1.20–1.44; EL 0.29–0.32; PW 1.24–1.40; PeW 0.51–0.64; PpW 0.60–0.74; HBaL 0.28–0.35; HBaW 0.08–0.12; CI 100.0–103.4; PI 96.7–102.8; PPeI 218.7–243.1; PPpI 189.2–206.7; HBaI 28.6–34.3.

G y n e (Fig. 183) (description of R. R. SNELLING, personal communication). - „Measurements (mm): HW (greatest head width below the eyes) 1.31–1.38, HL (greatest length from the lower margin of the frontal lobes to the highest level of the margin of the vertex) 11.55–1.58; TL 6.5–6.7.

Head more slender than that of the major, 1.13–1.18 times as long as wide, otherwise about as described for soldier. Each ocellus placed in deep pit; distance between lateral ocelli about 1.3 times distance between anterior ocellus and either lateral ocellus; lateral ocelli removed from vertexal margin by about twice their diameter.

Mesosomal segmentation normal fro *Cephalotes* females; pronotum about as described for major but transverse carina less distinct; mesoscutum and scutellum flat, reticulate-foveate, each fovea with appressed, glittering scale-like seta; basal face of propodeum angularly produced on each side; sculpture of basal face like that of mesoscutum; declivity dull and granulopunctate. Side of pronotum about as in major; mes- and metepisterna and side of propodeum dull and granulopunctate; anepisternum with abundant appressed, glittering, scale-like setae; katepisternum with anterior tooth-like tubercle; patches of appressed, glittering, scale-like setae on katepisternum above and along posterior margin and along posterior margin of metepisternum. Legs as in soldier.

Petiole with lateral spine very short and acute; otherwise petiole and postpetiole about as described for major.

Metasomal tergum 1 about 1.4 times as long as wide; gaster otherwise as described for major.

Color about as in major but frontal disc with large dark brown to blackish infuscation in center and mesosoma almost entirely blackish (except pronotum variably marked with reddish)."

Measurements (in mm) and indices: TL 6.52–7.24; HL 1.40–1.48; HW 1.36–1.40; EL 0.32–0.36; PW 1.32; PeW 0.54–0.57; PpW 0.71–0.77; HBaL 0.40–0.44; HBaW 0.12–0.13; CI 94.6–97.1; PI 103.0–106.1; PPeI 231.6–244.4; PPpI 171.4–185.9; HBaI 29.5–30.0.

M a l e (Fig. 184) (description of R. R. SNELLING, personal communication). - „Measurements (mm): HW (greatest head width above the eyes) 0.76 - 0.79, HL (greatest length from the lower margin of the frontal lobes to the highest level of the margin of the vertex) 0.67 - 0.71; TL 4.1–4.2.

Head 1.07–1.19 times as broad as long; in frontal view vertex strongly elevated above level of upper eye margin; distance between inner eye margins about 1.8 times eye length; inner eye margins convergent below. Interocellar distance about 1.5 diameter of anterior ocellus; ocellocular distance about 2 times diameter of anterior ocellus. Antennal scape slightly longer than broad; third antennal segment about twice as long as broad and about 1.3 times length of fourth. Clypeus moderately convex; apical margin broadly, shallowly concave. Mandible with one distinct preapical tooth and 3–4 minute denticles basad of preapical tooth. Entire head contiguously micropunctate and dull, with widely scattered shallow foveae, especially on gular area, the bottoms of which are shiny.

Mesosoma normal for *Cephalotes* and without spines or tubercles. Dorsum of pronotum slightly shiny and moderately tessellate. Median lobe of mesoscutum mostly smooth and shiny, but distinctly tessellate anteromedially and with sparse, shallow, coarse foveae; posterior lobes dull and roughened between shallow, irregular foveae. Scutellum finely lineopunctate and slightly shiny. Metanotum and basal face of propodeum slightly shiny and contiguously micropunctate, propodeum also with several widely spaced, fine, longitudinal rugulae. Side of mesosoma shinier, very weakly and shallowly micropunctate and with extensive smooth areas, especially on mesepisternum.

Petiole and postpetiole nodes very low, petiole with short anterior face; discs of both segments smooth and shiny.

Metasoma shiny, segments smooth to superficially and irregularly tessellate."

Genitalia and subgenital plate as in Fig. 185.

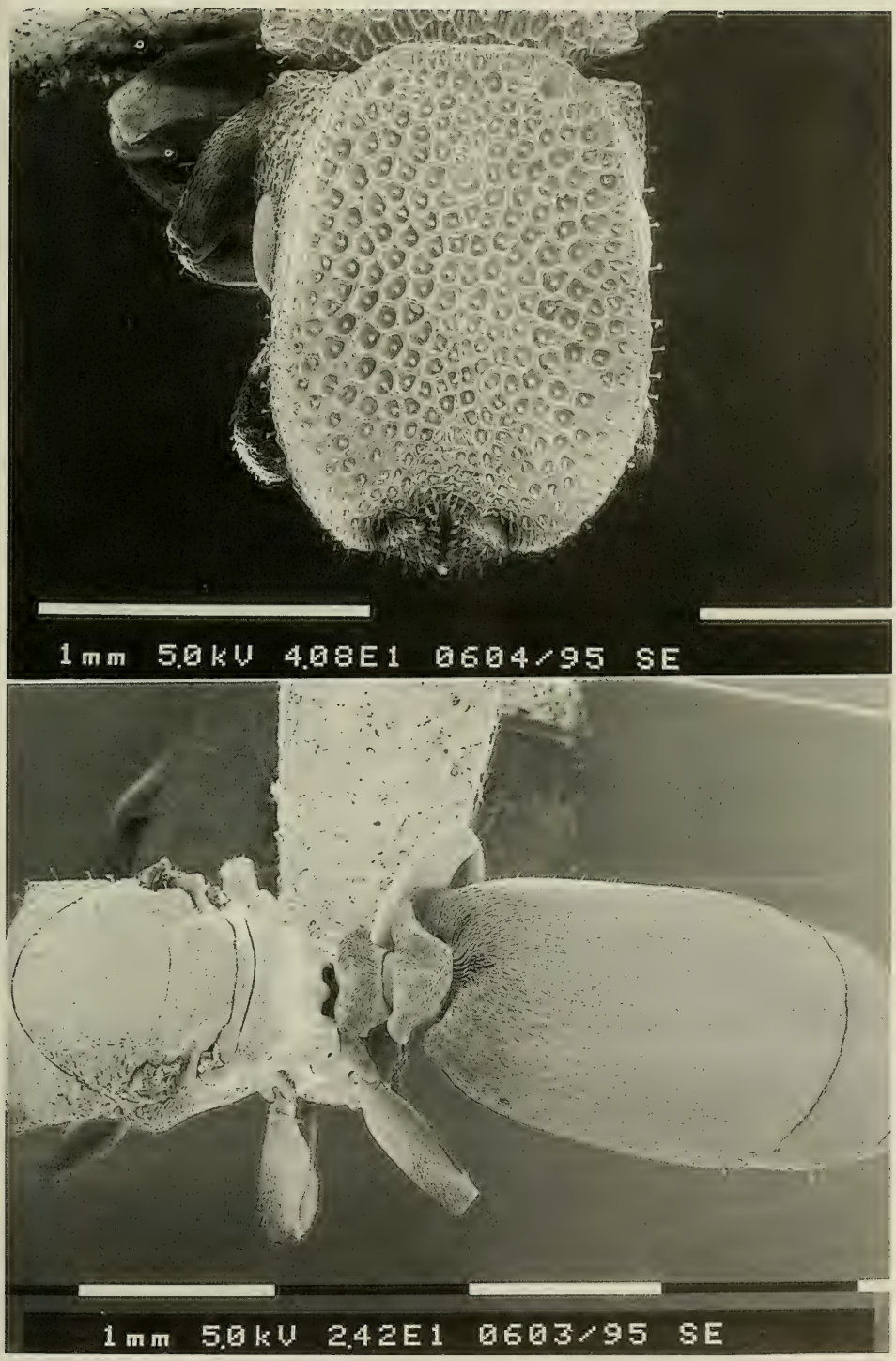


Fig. 183. *Cephalotes kukulcan* SNELLING. Gyne from Turneffe Island, Belize: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 184. *Cephalotes kukulcan* SNELLING. Male from Man-O-War Kay, Belize: head (top) and meso- and metasoma (bottom) in dorsal view.

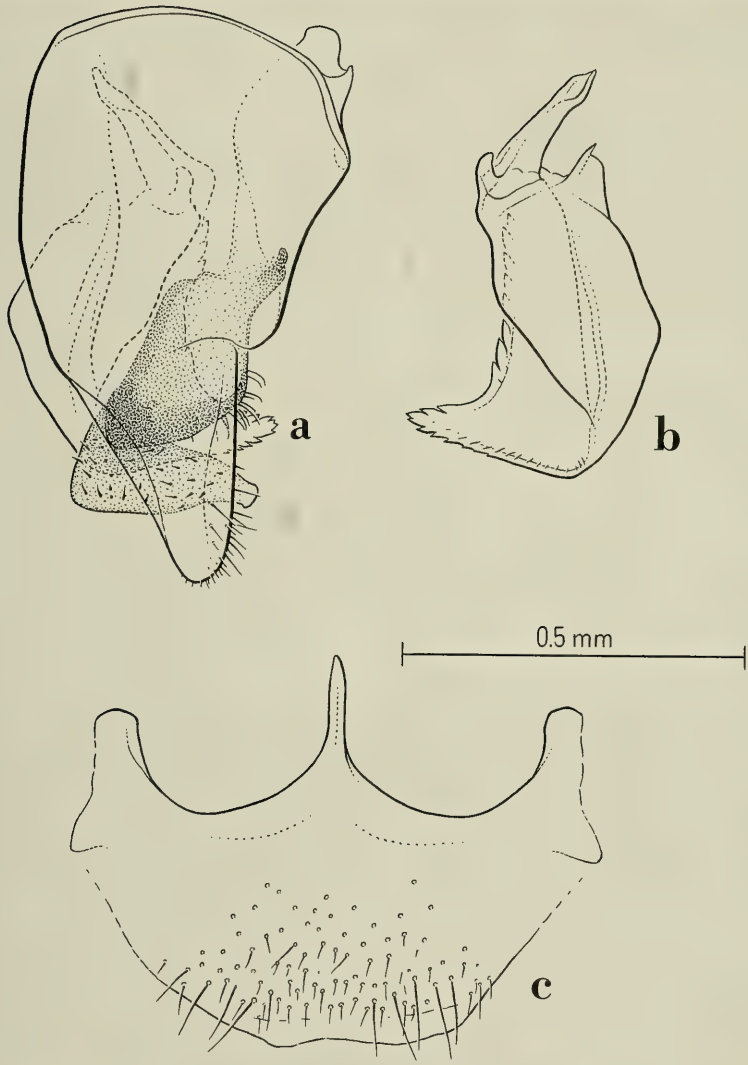


Fig. 185. *Cephalotes kukulcan* SNELLING. Male from Man-O-War Kay, Belize. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Measurements (in mm) and indices: TL 4.14–4.26; HL 0.65; HW 0.80; EL 0.35–0.36; PW 0.96; PeW 0.26–0.29; PpW 0.34–0.35; HBaL 0.42; HBaW 0.06–0.07; CI 123.1; PI 83.3; PPeI 331.0–369.2; PPpI 274.3–282.3; HBaI 14.3–16.7.

Material examined. - **Mexico**: Quintana Roo: 10 km S Boca Paila, 09.XII1985, 2 soldiers and 3 workers, J. F. LYNCH (LACM).

Belize: no further locality, 07.VIII.1928, 1 worker [USNM]. Stann Creek District, Twin Cays, 16.I.1987, 2 gynes (paratypes), 13 soldiers (holotype and 12 paratypes) and 22 workers (paratypes), J. F. LYNCH (LACM); 3 soldiers and 3 workers, 3 males, Man-O-War Cay, 03.VI.1985; 1 gyne, 1 worker, 1 male, Ragged Cay, 25.VI.1985; 2 soldiers and 7 workers, „Jellyfish Cay", Blue Ground Range, 31.V.1985; 1 gyne, 2 soldiers and 18 workers, North Grand

Bogue Cay, Turneffe Atoll, 29.III.1993. All paratypes and divided between BMNH, LACM, MCZC, and USNM.

D i s c u s s i o n . - *C. kukulcan* could be easily confused with *scutulatus* but the shape of the frontal carinae over the eyes and the width of the expansions of the mesosoma allow a sure separation of the two species. Another important trait useful to separate the workers of the two species are the body foveae, denser in *kukulcan* than in *scutulatus*. The males of both species are extremely similar to each other but the aedeagi reveal paramount differences (see Figs. 185 and 190).

As a matter of fact, the soldier of *kukulcan* is much more similar to that of a new species described in this paper as *liepini* than to the soldier of *scutulatus*. The differential characters between these two species are given under the diagnosis of *liepini*.

If our tentative attribution to this species of the specimen figured by LONGINO & COLWELL (1996) is correct, its range should include the Costa Rica as well.

D i s t r i b u t i o n : Mexico, Belize, Costa Rica?.

Cephalotes scutulatus (SMITH) new combination
Figs. 186, 187, 188, 189, 190

Cryptocerus scutulatus SMITH, 1867: 524 pl. 26, figs. 3, 3 a. Soldier. Original description. Type locality: Mexico. Type material: holotype (syntype?) soldier labelled „Mex., *Cryptocerus scutulatus*. Smith. Trans. Ent. Soc., Type" in OXUM (Hymenoptera type 1043), examined plus two possible syntypes (almost certainly from the same series), worker and soldier labelled „7., Mex., Collect. G. Mayr, *notatus* [no handwriting of Mayr], G. Mayr, Type.", in NHMW, examined.

Cryptocerus angulosus SMITH, 1867: 524, figs. 7, 7a. Worker. Original description. Type locality: Mexico. Type material: holotype worker labelled „Mex., *Cryptocerus angulosus*. Trans. Ent. Soc., Type" in OXUM (Hymenoptera type 1046), examined. Synonymy by EMERY, 1922: 311.

Cryptocerus jucundus SMITH, 1876: 606, pl. 11, fig. 3. Worker. Original description. Type locality: Mexico. Type material: holotype worker (without head) in BMNH, examined. Synonymy by EMERY, 1890: 76.

Cryptocerus angulosus SMITH, WHEELER, 1907 b: 273, figs. 1–3. Worker, soldier, male.

Cryptocerus angulosus SMITH, WHEELER, 1910: fig. 78 Worker, soldier.

Paracryptocerus scutulatus (SMITH), KEMPF, 1952: 26, figs. 4, 8. Worker, soldier. First combination in *Paracryptocerus*.

Zacryptocerus scutulatus (SMITH), HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *pinelii* clade distinguished by the following combination of characters: in the worker, frontal carinae strongly upturned over the eyes, pronotal and propodeal sides with a broad membranaceous border incised anteriorly, petiole and postpetiole with pointed spines, and, in the soldier and gyne, floor of the disc with superficial and not contiguous foveae, and black (not brown) dominant coloration.

W o r k e r (Fig. 186) (description of KEMPF, 1952). - „Length 3.5–4.0 mm. Black; frontal carinae, occipital corners, lateral border of thorax, spines of petiole and postpetiole, anterolateral corners of first gastral tergite, knees, outer face of tibiae sordid or brownish white. Antennae and tarsi ferruginous.

Head subquadrate, the maximum length subequal to the interocular width. Frontal carinae and the rounded or subangulate occipital corners membranaceous. Sides of head upturned and projecting above the eyes. Greatest diameter of eyes less than one fourth of maximum length of head.

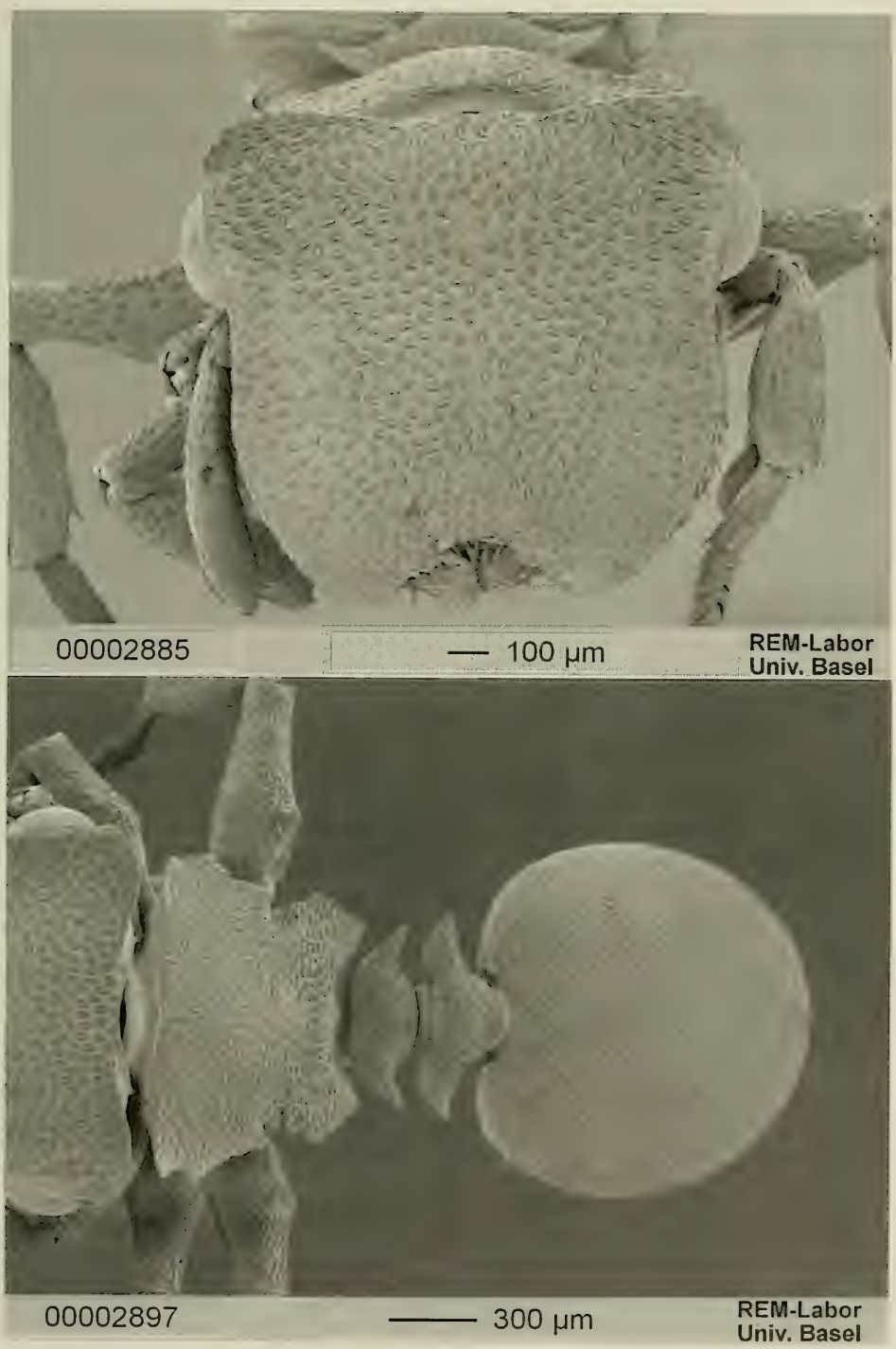


Fig. 186. *Cephalotes scutulatus* (SMITH). Worker from Chimaltenango, Guatemala: head (top) and meso- and metasoma (bottom) in dorsal view.

Thorax narrower than head, somewhat longer than wide; the anterior border convex. Pronotum and epinotum with a membranaceous border on each side, each with a notch just behind its anterior corner. Mesonotum produced on each side into a short spine. Mesoepinotal suture indistinct, especially mesially. Hind femora not marginate above.

Peduncular segments with well-developed, partly membranaceous and recurved lateral spines, those on petiole being, however, distinctly narrower, more acute and less flattened than those on postpetiole. Anterior face of petiole perpendicular to the dorsal face, not impressed.

Gaster cordate-elliptical, comparatively short, the first gastral tergite with a membranaceous, evenly rounded border on the anterolateral lobes.

Opaque; finely and densely shagreened. Head, thorax and peduncle with squamiferous foveolae, which are at most vestigial on gaster. Hairs glistening white, very short, scale-like and appressed, one to each foveola on head and thorax, much smaller and denser on remainder of the body."

Measurements (in mm) and indices: TL 4.52–4.56; HL 1.10–1.12; HW 1.30–1.34; EL 0.32; PW 1.12–1.16; PeW 0.68–0.72; PpW 0.80; HBaL 0.40; HBaW 0.09–0.10; CI 118.2–119.6; PI 115.5–116.1; PPeI 155.5–170.6; PPpI 140.0145.0; HBaI 22.5–25.0.

S o l d i e r (Fig. 187) (description of Kempf, 1952). - „Length 4.5–6.5 mm. Black; cephalic disc, and shoulders brownish yellow. Scapes, basal funicular segments, and tarsi ferruginous. Lateral borders of epinotum, spines of petiole and all, but a lozenge-shaped area on the disc of the first gas tral tergite, sordid-white, as are also the posterior borders of the remaining gastral tergiters.

Head about as long as wide, longer than thorax. Supramandibular excision broad, not semicircular. Cephalic disc subquadrate, with rounded corners. Edge of disc and the part overlying the antennal scrobe, submembranaceous. Edge upturned, glassy, and crenulate. Median portion of disc distinctly convex. Occipital lobes turned upward apically, irregularly crenate. Sides of head not separated from the truncate occiput by a ridge or margination.

Thorax wider than long. Pronotum much wider than meso- and epinotum, the latter two subequal in width. Anterior border of pronotum slightly arched, shoulders and sides of pronotum membranaceous and crested. Transverse pronotal carina strongly crested, narrowly interrupted in the middle. Mesonotum produced on each side into a short, sharp angle. Sides of epinotum narrowly crested, except in front where it is suddenly narrowed and produced into a small rounded lobe.

Peduncular segments as in worker, but somewhat stouter, the postpetiole much wider than the petiole.

Gaster as in worker, scarcely longer than broad, bluntly pointed behind.

Subopaque; upper face of head shining. Head and thorax foveolate, the former more coarsely and much more sparsely so, especially on the concave portions of the cephalic disc. Petiole, postpetiole, gaster, and legs finely and densely shagreened. Hairs as in worker."

Measurements (in mm) and indices: TL 5.36–6.00; HL 1.40–1.48; HW 1.56–1.64; EL 0.32; PW 1.60–1.72; PeW 0.72–0.76; PpW 0.84–0.86; HBaL 0.40–0.44; HBaW 0.11–0.12; CI 110.8–111.4; PI 95.3–97.5; PPeI 222.2–226.3; PPpI 190.5–200.0; HBaI 27.3–27.5.

G y n e . - Head broader than long, subquadrate. Head dorsum flat to gently convex medially. Frontal carinae deeper than the rest of the head. Borders of the frontal carinae superficially and sparsely crenulate, raised anteriorly and slightly higher or in the same plane as the floor of the disc posteriorly. Vertexal angles obtuse and with broad, crenulate lamellae. Eyes visible in full dorsal view. Ocelli close to the posterior border of the head disc. Mandibles with a lateral carina.

Mesosoma. Humeral angles with a pair of obtuse, lamellaceous teeth with crenulate margins, converging posteriorly and connected with the narrow pronotal carina. Pronotal sides superficially marginate and straight posteriorly. Promesonotal suture impressed. Lower

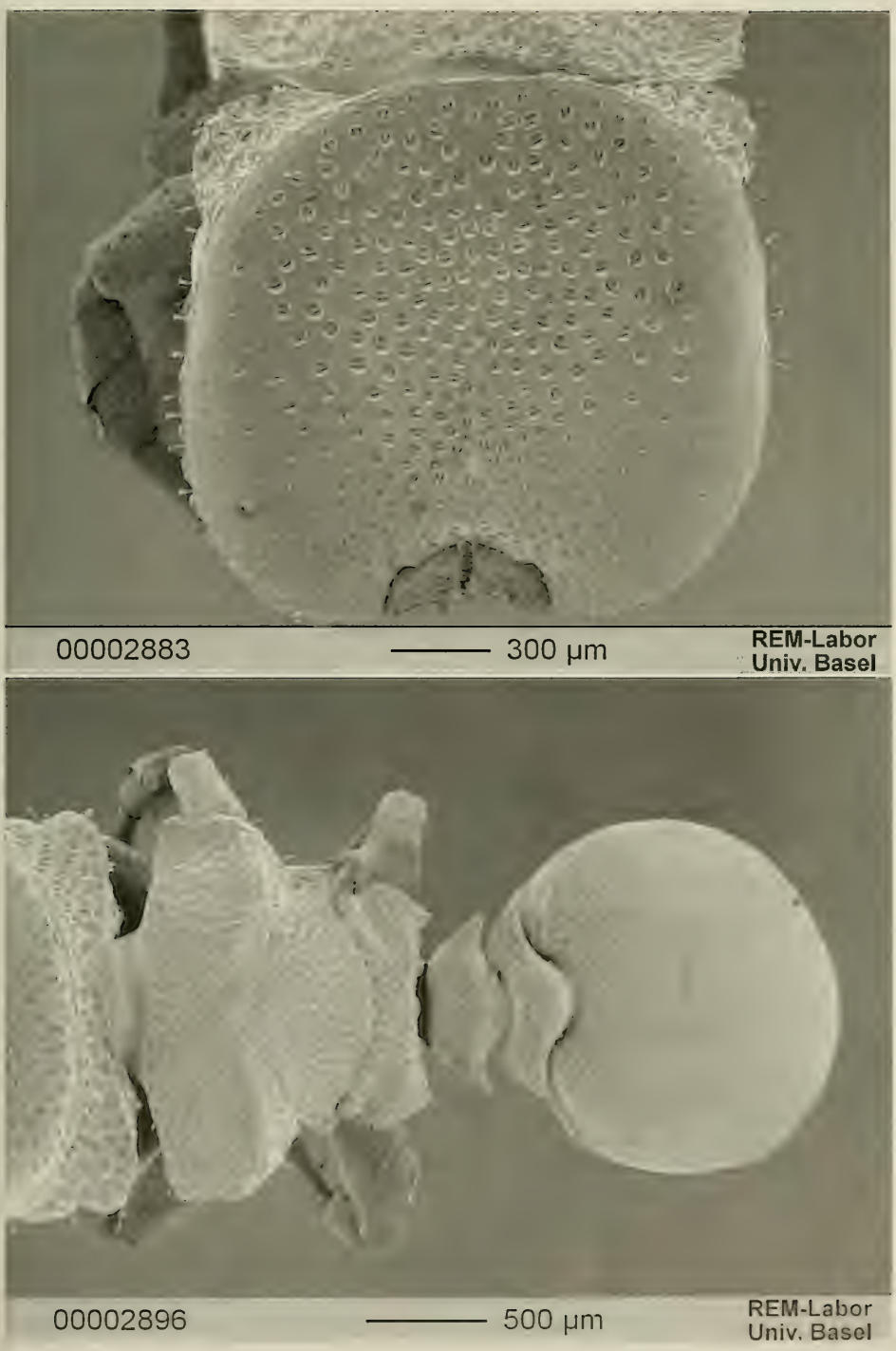


Fig. 187. *Cephalotes scutulatus* (SMITH). Soldier from Belize (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

mesopleurae with a denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face with a pair of broad, triangular or round teeth strongly converging posteriorly; declivous face narrowing posteriorly and with a superficial, lateral margin.

Petiole with oblique and slightly concave anterior border; its sides with a pair of teeth. Postpetiole broadly convex and with a pair of dorso-lateral, large spines pointed backwards.

Gaster with broad lobes either marginate or with a narrow lamella.

Legs. Hind femora superficially angulate. Mid and hind basitarsi almost flat and constantly subequal in width.

Wings as in Fig. 188.

Sculpture. Head dorsum minutely and superficially punctate, with superficial, variably clumped foveae diminishing in size anteriorly, shallower and rare on the frontal carinae, denser in smaller specimens. Ventral part of the head punctate and with sparse, shallow, irregular foveae. Pronotum with sculpture similar to the one of the head dorsum. Mesonotum and scutellum reticulate and with superimposed dense foveae of variable size, denser on the scutellum. Basal face of the propodeum and anterior fourth of its declivous face densely and irregularly foveolate. Pleurae reticulate. Propleurae with longitudinal rugosities on the center. Mesopleurae with small, slightly irregular foveae, denser on the upper part. Metapleurae with few, longitudinal rugae on the ventral border and with foveae as those of the mesopleurae only in the center. Petiole, posteriorly, and postpetiole with sculpture similar to the basal face of the propodeum but the foveae shallower. Remaining parts of the declivous face of the propodeum and anterior half of the petiole and gaster minutely reticulate. Anterior third of the first gastral tergite with thin, longitudinal rugosities or with very superficial, irregular foveae separate by irregular, thin rugosities. Posterior half of the first gastral sternite superficially shining. Legs reticulate; distal part of the femora and outer face of the tibiae with minute, irregular foveae.

Pilosity. Each fovea with an appressed, canaliculate hair. Frontal carinae, margin of the vertexal angles, mesonotum, pedicel, gaster and legs with erect, weakly clubbed hairs. Sternites with sparse, long, thin, slightly pointed hairs. Body parts without foveae with sparse, short, appressed hairs.

Colour. Black. Dorsal half of the head or at least the frontal carinae and the posterior border of the disc orange. Floor of the disc black, occasionally maculate. Pronotal sides with an orange spot extending sometimes to the dorsum. First gastral tergite with two pairs of broad, yellow-orange spots. Outer face of the tibiae dark orange to light brown.

Measurements (in mm) and indices: TL 6.32–7.48; HL 1.48–1.56; HW 1.54–1.64; EL 0.35–0.36; PW 1.56–1.60; PeW 0.67–0.72; PpW 0.89–1.00; HBaL 0.50–0.56; HBaW 0.14–0.15; CI 104.0–105.1; PI 98.7–102.5; PPeI 219.7–238.8; PPpI 160.0–175.3; HBaI 25.9–28.0.

M a l e (Fig. 189). - Head (eyes included) 1/3 broader than long. Vertex protruding dorsally and bearing salient ocelli; vertexal angles converging towards the pair ocelli. Compound eyes broadly convex. Frontal carinae not raised, diverging backwards, not reaching the median ocellus posteriorly but almost reaching the eyes. Frons flat. Clypeus gently convex posteriorly and incised anteriorly. Mandibles short; their external face with salient carina. Antennae short. Scapes thick, twice as long as the first funicular joint; remaining funicular joints, stout and slightly thickening apically.

Mesosoma robust. Pronotum in dorsal view with the sides gently diverging backwards. Mesonotal scutum convex in side view; median Mayrian furrow almost absent Basal and declivous faces of the propodeum differentiate; basal face dorsally weakly convex, laterally unarmed and with the sides converging posteriorly; declivous face with the sides superficially carinate and converging posteriorly. Petiole narrower than the postpetiole; its anterior face concave. Petiolar sides with or without a minute pair of lateral denticles converging posteriorly. Sides of the postpetiole with another minute pair of denticles.

Gaster narrower than the mesosoma.

Genitalia and subgenital plate as in Fig. 190.

Wings as in the gyne.

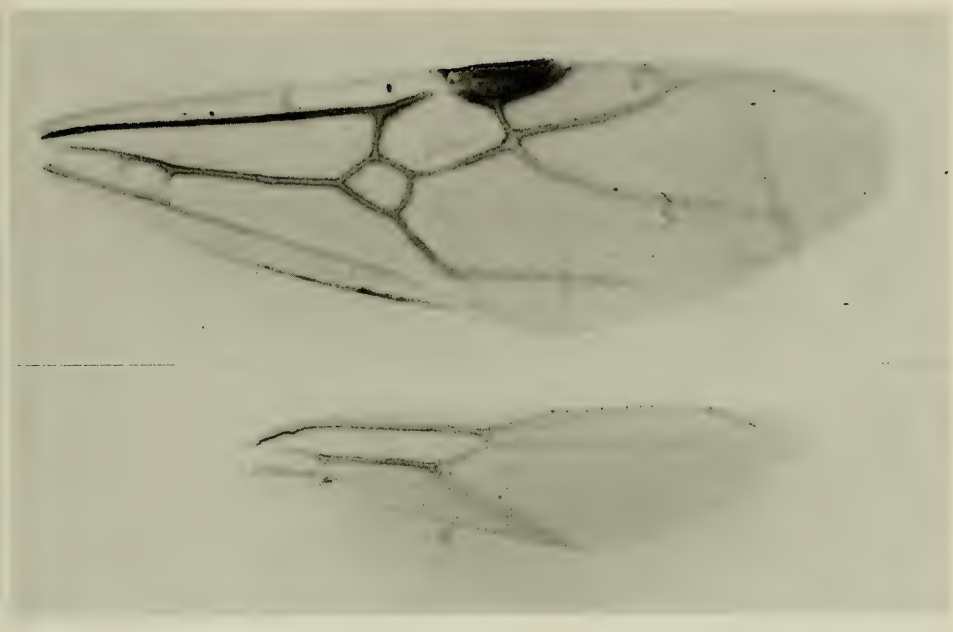


Fig. 188. *Cephalotes scutulatus* (SMITH). Gyne from Trece Aguas, Guatemala, fore and hind wings.

Sculpture. Head dorsum minutely reticulate-punctate and with sparse, small, shallow, irregular foveae and wit irregular rugosities. Pronotum superficially reticulate and with sparse, shallow foveae. Basal face of the propodeum reticulate and irregularly foveolate-rugulose. Pleurae reticulate; mesopleurae with small, superficial foveae on the center; metapleurae with few, irregular, longitudinal rugosities. Pedicel and first gastral tergite reticulate; this sculpture but more superficial and slightly shining on the remaining tergites, on the sternites and on the legs.

Pilosity. Body with three types of hairs: (1) suberect, long, thin, pointed hairs dense on the head, on the mesosoma, sparse on the pedicel, on the gaster and on the legs; (2) shorter than the cephalic hairs, decumbent on the gaster and on the legs, denser on the legs; (3) short, pointed, decumbent on the funiculi.

Colour. Dark brown to black with lighter coxae, pedicel and gaster. Legs yellowish with darker proximal part of the femora.

Measurements (in mm) and indices: TL 4.68–4.72; HL 0.72–0.76; HW 0.92–0.94; EL 0.40; PW 1.08; PeW 0.37–0.38; PpW 0.41–0.46; HBaL 0.47–0.51; HBaW 0.07–0.08; CI 123.7–127.8; PI 85.0–87.0; PPeI 242.1–254.0; PPpI 200.0–229.3; HBaI 14.9–15.7.

Material examined. - **Mexico**: without further locality, 1 worker (holotype of *angulosus*) [OXUM], 1 soldier (holotype) [OXUM], 1 worker and 1 soldier (probably from the same series and labelled as types of *notatus* Mayr) [NHMW]; without further locality, 03.III.1958, intercepted in Texas, Brownsville, on Bromeliads, 1 soldier, HEINRICH [USNM]; Tuxtepec, April, 1 worker, W. M. MANN [USNM]. Vera Cruz: Pueblo Nuevo nr. Tetzonapa, 13.VIII.1953, 1 worker, E. O. WILSON [MCZC]; Vera Cruz, XI.1963, 2 workers, N. L. H. KRAUSS [USNM]; same locality, III, VI.1965, 6 workers, 1 gyne, N. L. H.

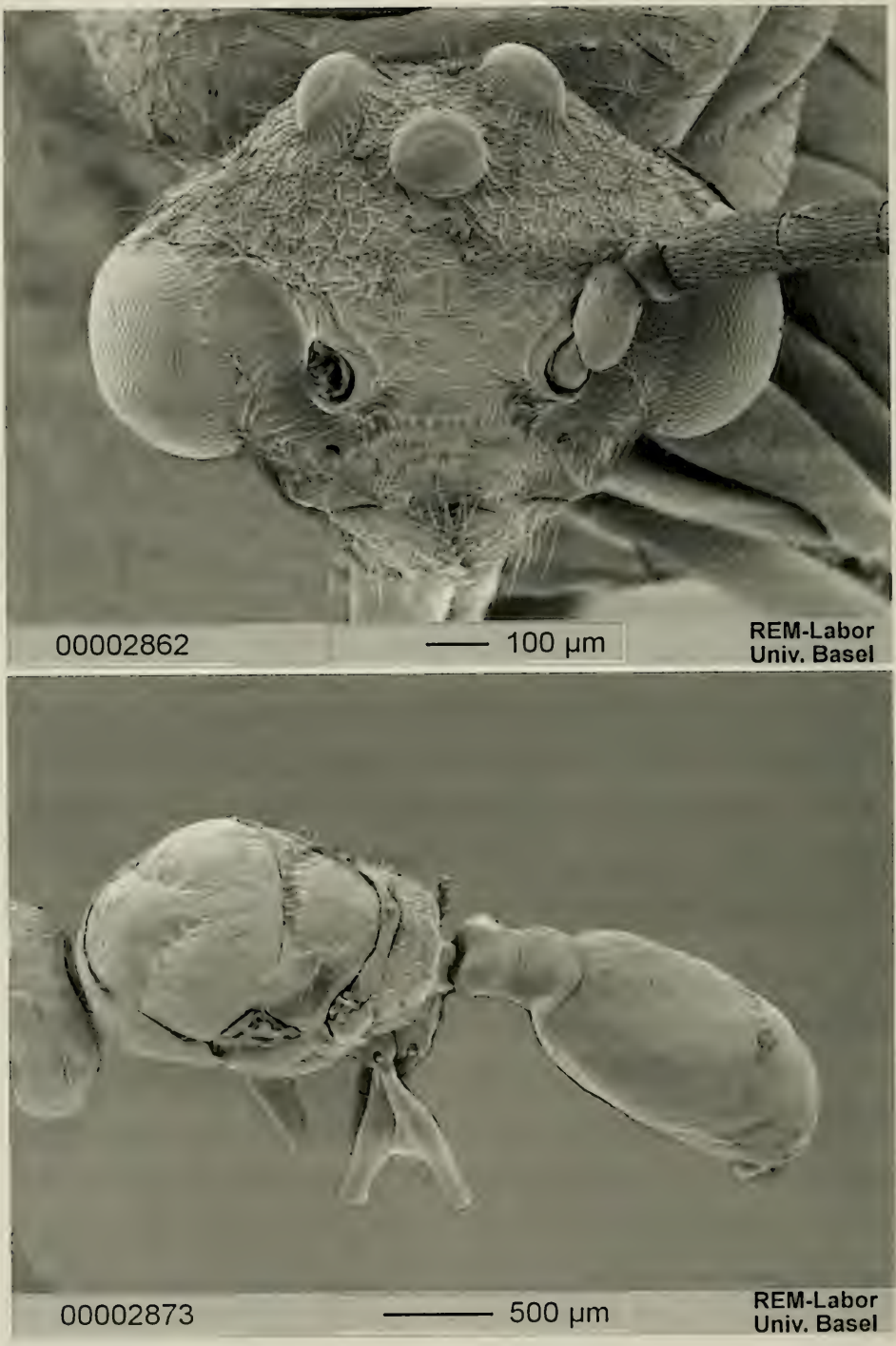


Fig. 189. *Cephalotes scutulatus* (SMITH). Male from Manatee, Belize: head (top) and meso- and metasoma (bottom) in dorsal view.

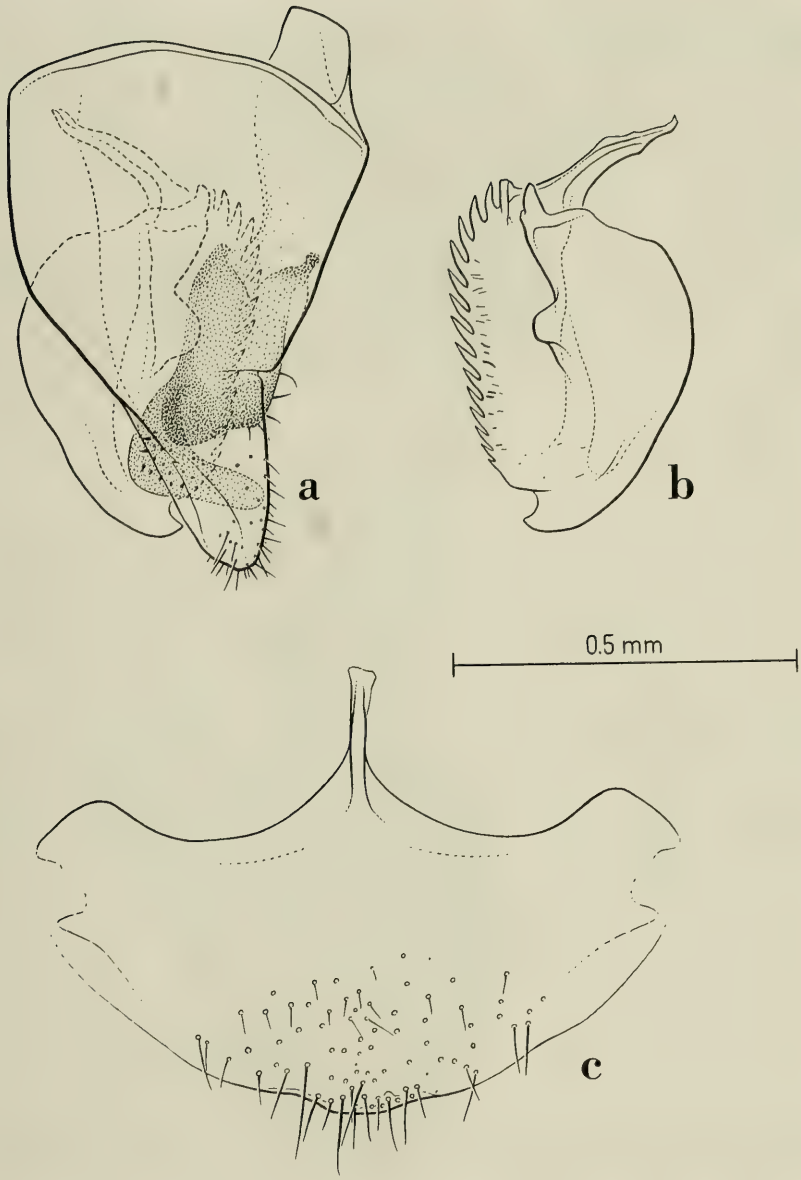


Fig. 190. *Cephalotes scutulatus* (SMITH). Male from Manatee, Belize. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

KRAUSS [USNM]; Catemaco, 29.V.1964, 1 worker, G. HALFTER & P. REYES [MZSP]; Orizaba, 1 worker [MHNG]. Guerrero: Highway 95, 59 mi N of Acapulco, 30.VII.1965, 1 worker [MCZC]. Chiapas: Ococingo, Laguna Ocotal Grande, ca. 950 m, 20.VII.–01.VIII.1954, 1 worker, 1 soldier, R. L. DRESSLER [MCZC]; Junction of Highways 190 & 195, 24.VI.1973, 1 worker, G. EKIS [USNM].

Belize: no further locality, 5 workers, 4 soldiers [MCZC, USNM]; Manatee, 12 workers, 2 soldiers, 5 males, J. D. JOHNSON [MHNG, MCZC]; Xunantunich, 1959, 1 worker, N. L. H. KRAUSS [USNM]; Augustine, VIII.1963, 1 worker, J. REISKIND [MCZC].

Guatemala: no further locality, intercepted on orchid, 13.VII.1937, 2 workers, 1 soldier [MZSP]; Zacapa, 13.XII.1911, 6 workers, 1 soldier, W. M. WHEELER [MCZC]; Trece Aguas, Alta V. Paz, 1 worker, SCHWARZ & BARBER [MCZC]; same locality, 1 gyne, BARBER & SCHWARZ [MCZC]; Petén, July 1984, 1 worker [JSHC]; Chimaltenango, Yepocapa, 13–20.II.1948, 1 worker, H. T. DALMAT [USNM]; Finca Conchita, 16.XII.1948, 1 worker, A. F. M. [USNM].

El Salvador: San Salvador, 07.VI.1958, 1 worker, O. L. CARTWRIGHT [USNM].

Costa Rica: unknown locality, 17.IV.1943, intercepted on orchids, 3 workers, 5 soldiers [MZSP, NHMB]; unknown locality, 1 worker [MHNG]; Alajuela, 28.XI.1911, 5 workers, 3 soldiers, W. M. WHEELER [MCZC, MZSP]; same locality, 1 worker, ALFARO [MCSN]; Puerto Viejo, Heredía, 08.VIII.1965, 1 worker, F. COYLE [MZSP]; Sirena, Penin. Osa, 8°28' N, 83°35' W, 50 m, 20.XII.1981, 2 workers, J. LONGINO [MCZC]; Bagaces, 4 workers [MCSN]; Nicoya, 5 workers, 1 gyne, R. ALFARO [MCSN].

Panama: Bugaba, 1 worker, Champion [MHNG].

Ecuador: Esmeralda: Zapallo Grande, 25–30.X.1987, 1 worker, M. HUYBENSZ [MCZC].

Discussion. - The worker of *scutulatus* is quite similar to *kukulcan* (q. v.) but can be separated from it by means of the characters already listed in the diagnosis. An interesting trait of *scutulatus* are the vertexal angles with broad, round, membranaceous expansions, a character it shares with the Dominican fossil *caribicus*. *Scutulatus* has been regarded as a very distinctive species within the *pinelii* clade (KEMPF, 1952: 26). Its morphological isolation, however, is greatly weakened now by the discovery of the new species *kukulcan*. The two species appear to coexist in narrow sympatry in Belize: on one occasion we received both species mounted on the same pin. This species is reported by KEMPF (1952) also from Venezuela and Colombia on the base of specimens intercepted on orchids of Venezuelan and Colombian provenance at U. S. quarantine stations. The Colombian distribution is reported also by FERNÁNDEZ et al. (1996).

Distribution: Mexico, Belize, Guatemala, El Salvador, Honduras, Costa Rica, Panama, Colombia, Venezuela, Ecuador.

† *Cephalotes caribicus* DE ANDRADE new species

Figs. 15 C, 191

Type material: Holotype worker in the Dominican amber sample Do–5383 in the SMNS; paratype worker in the Dominican amber sample GOPC-5 in the GOPC.

Derivatio nominis: *caribicus* is a neologism referring to the area of provenance of this species.

Diagnosis. - A member of the *pinelii* clade differing from its sister species, *incertus*, by the worker with the first gastral tergite with broad anterolateral membranaceous expansions but without true lobes.

Worker (Fig. 191). - Head broader than long. Frontal carinae very weakly crenulate only in their anterior part. Vertexal angles broad, round and membranaceous. Mandibles laterally carinate. Antennal club two-jointed.

Mesosoma. Scapular angles absent. Anterior pronotal border convex; pronotal sides with a broad, membranaceous expansion, subtruncate anteriorly and narrowing posteriorly.

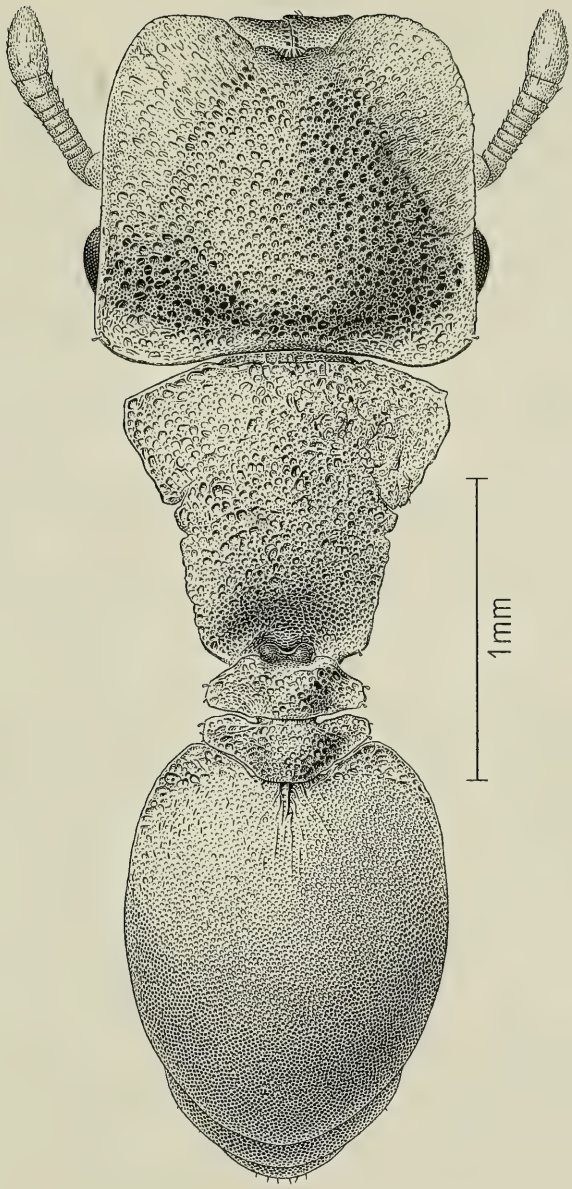


Fig. 191. *Cephalotes caribicus* DE ANDRADE from Dominican amber. Worker in dorsal view. Appendages omitted.

Promesonotal suture absent. Mesonotum with a pair of lateral, truncate, teeth narrowly separate from the pronotal and propodeal expansions. Propodeal suture superficially impressed on the sides only. Declivous face of the propodeum gently sloping backwards. Basal and declivous faces of the propodeum with a narrow, membranaceous expansion originating cranially on the basal face and slightly narrowing backwards.

Petiole with the anterior face deeply concave and with a pair of small dorsal swellings; petiole dorsally and anteriorly depressed; its sides with a broad, round, wing-shaped, membranaceous expansion directed laterally. Postpetiole with a comparably broad, wing-shaped, membranaceous expansion rounded apically and directed laterally.

Gaster suboval and with broad, anterolateral, membranaceous expansions.

Hind femora angulate. Mid and hind basitarsi with flat and extremely broad base.

Sculpture. Head dorsum minutely punctate, with small, superficial foveae variably clumped, sparser and shallower on the frontal carinae. Ventral part of the head minutely reticulate-punctate. Mesosoma and pedicel reticulate-punctate and with foveae, sparser on the propodeum. First gastral tergite and legs reticulate, the same type of sculpture but more superficial on the first gastral sternite.

Pilosity. Body foveae with appressed hairs. Borders of the vertexal angles, of the propodeum, of the pedicel and posterior borders of the second and third gastral tergites with rare, short clubbed hairs. Gaster and legs with sparse, thin, short, appressed hairs. Second gastral sternite with a pair of long, erect, pointed hairs.

Colour indistinguishable (both specimens are covered by a thin gaseous film). Frontal carinae, vertexal angles and membranaceous expansions semitransparent.

Measurements (in mm) and indices: TL 3.97–4.64; HL 0.98–1.04; HW 1.27–1.32; EL 0.23–0.25; PW 1.04–1.18; PeW 0.52; PpW 0.55; HBaL 0.30–0.34; HBaW 0.15; CI 126.9–129.6; PI 111.9–122.1; PPeI 200.0–226.9; PPpI 189.1–214.5; HBaI 46.9–50.0.

Material examined. - **Dominican amber:** 1 worker, holotype, (reference number: Do–5383) [SMNS]; 1 worker, paratype, (reference number: GOPC–5) [GOPC].

Discussion. - *C. caribicus* shares, synapomorphically, with the Recent Brazilian *incertus* the pronotal crest followed by a close mesonotal tooth and the petiole bidentate dorsally. It is noteworthy that its discovery appears to suggest Brazilian Chaco affinities previously unknown for the Dominican amber fauna. We suppose, however, that the discovery of the other castes of *caribicus* is likely to show additional differences between the two species. *Caribicus* is the sole known fossil member of the *pinelii* clade and it appears to be a very distinctive species both within the clade and among the other fossils.

Distribution: Dominican amber.

Cephalotes incertus (Emery) new combination
Figs. 192, 193

Cryptocerus incertus Emery, 1905: 171, fig. 31. Worker. Original description. Type locality: Corrientes (Argentina). Type material: holotype worker labelled „Corrientes, 15.VI.900" [MCSN], examined

Paracryptocerus incertus (Emery), Kempf, 1952: 15, figs. 1, 16. Gyne. First combination in *Paracryptocerus*.

Zacryptocerus incertus (Emery), Kempf, 1974: 71, fig. 2. Soldier. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *pinelii* clade differing from its sister species, *caribicus*, by the lobate gaster of the worker.

Worker (Fig. 192) (description of Kempf, 1952). - „Length 4.0 mm. Median head length 0.90 mm. Weber's length of thorax 1.10 mm. Ferruginous; the head slightly darker. Membranaceous borders of thorax and the frontal carinae pale yellow-ferruginous.

Head subquadrate, longer than wide (45:39), as long as thorax. Sides of head straight, not upturned above eyes. Occipital corners rounded, not membranaceous. Occipital border scarcely emarginate. Greatest diameter of eyes less than one fourth of maximum head length.

Thorax longer than wide across the pronotum. Membranaceous border of pronotum and epinotum much narrower than in the other species of the group. Anterior angle of pronotum obtuse, the sides converging caudad. Mesonotum with a broad, blunt, more or less rounded, marginate lobe on each side. Mesoepinotal suture obsolete mesally. Epinotum as broad as mesonotum, narrower than pronotum. Declivous face differentiated from basal face. Hind femora not longitudinally marginate nor crested above the apical half.

Peduncular segments massive. Petiole excavate antero-mesally, with narrowly crested lateral lobe. Postpetiole with an elliptical, membranaceous lobe on each side, the lobes constricted at their base.

Gaster longer than broad, ovate, broadest behind the half of its length. Anterolateral lobes angulate and narrowly crested.

Subopaque, finely shagreened. Dorsum of head, thorax and peduncular segments foveolate, each foveola containing an elongate, oval, canaliculate, golden, appressed scale. No erect setae on the first gastral tergite."

Measurements (in mm) and indices: TL 3.44–4.38; HL 0.80–0.96; HW 0.80–1.04; EL 0.20–0.24; PW 0.70–0.90; PeW 0.37–0.50; PpW 0.40–0.55; HBaL 0.23–0.26; HBaW 0.07–0.10; CI 100.0–108.3; PI 114.3–115.5; PPeI 180.0–189.2; PPpI 163.6–175.0; HBaI 30.4–38.5.

S o l d i e r (Fig. 193) (description of Kempf, 1974). - „Total length 4.5 mm; head length 1.24 mm; head width 1.27 mm; Weber's length of thorax 1.35 mm; width of pronotum 1.27, of mesonotum 0.84, of propodeum 0.73 mm; length and width of petiole 0.26 and 0.49 mm; length and width of postpetiole 0.25 and 0.53 mm; maximum width of gaster 1.11 mm. Ferruginous; mandibles fuscous brown; subtranslucid portion of head disc above antennal scrobe, membranaceous margins of pronotum and propodeum, and lateral appendages of petiole and postpetiole yellowish brown.

Head quadrate, scarcely broader than long. Cephalic disc deeply emarginate above mandibles, anterolaterally evenly rounded, postero-laterally obliquely truncate, posteriorly vestigially between a pair of faint and blunt teeth; rim of disc scarcely crenulate, never glassy nor translucid, obliquely upturned on sides; disc proper gently transversely convex in the middle behind clypeus, moderately concave postero-latrally at level of eyes; clypeal and frontal sutures more or less distinct. Occipital lobes rectangular with sharply carinate margins and a faint carina extending from the occipital corner upward to disc, but fading out before reaching the rim of the latter, separating the lateral faces from the occipital face of head below disc. Inferior border of cheeks continued backwards below eyes and distinctly marginate.

Thorax longer than maximum width of pronotum. Anterior border of the latter straight in the middle, gently deflected caudad on lateral sixth on both sides; lateral corner rectangular, scarcely excavate, narrowly membranaceous; transverse pronotal carina blunt and low, narrowly interrupted in the middle. Promesonotal suture distinct. Mesonotum less than twice as broad as long, the prominent lateral lobes bluntly rounded at apex to obtusely angulate. Metanotal suture indistinct. Propodeum with narrow, membranaceous lateral borders, the border slightly constricted just behind the anterior corner, setting off a shorter membranaceous lobe; at the junction of the basal with the declivous face the border contains a low, solid denticle pointing upward; declivous face shallowly excavate above petiolar insertion. Base of fore coxae anteriorly not drawn out into a pointed cone. Hind femora bluntly angulate above, but without a longitudinal crest on apical half. First tarsomere of hind legs compressed and broadened, shorter than the remaining four tarsomeres combined.

Pedicellar segments rather stout and solid. Petiole as long as postpetiole, antero-mesially excised, laterally with a short, posteriorly strongly deflected apically bluntly pointed membranaceous lobe (as in worker). Postpetiole slightly broader than petiole, with an elliptical membranaceous lobe on each side, the lobes constricted at their base. Gaster much longer than broad, the anterolateral lobes drawn out and mesially angulate to subdentate, not membranaceous.

Integument opaque to subopaque throughout, finely reticulate-punctate. Cephalic disc slightly shining due to superficial microsculpture, with sparse, shallow, oval, squamiferous foveolae; the minimum diameter of the latter subequal to distance between the foveolae. Sides and occiput similarly sculptured, microsculpture stronger, foveolae more crowded; the same

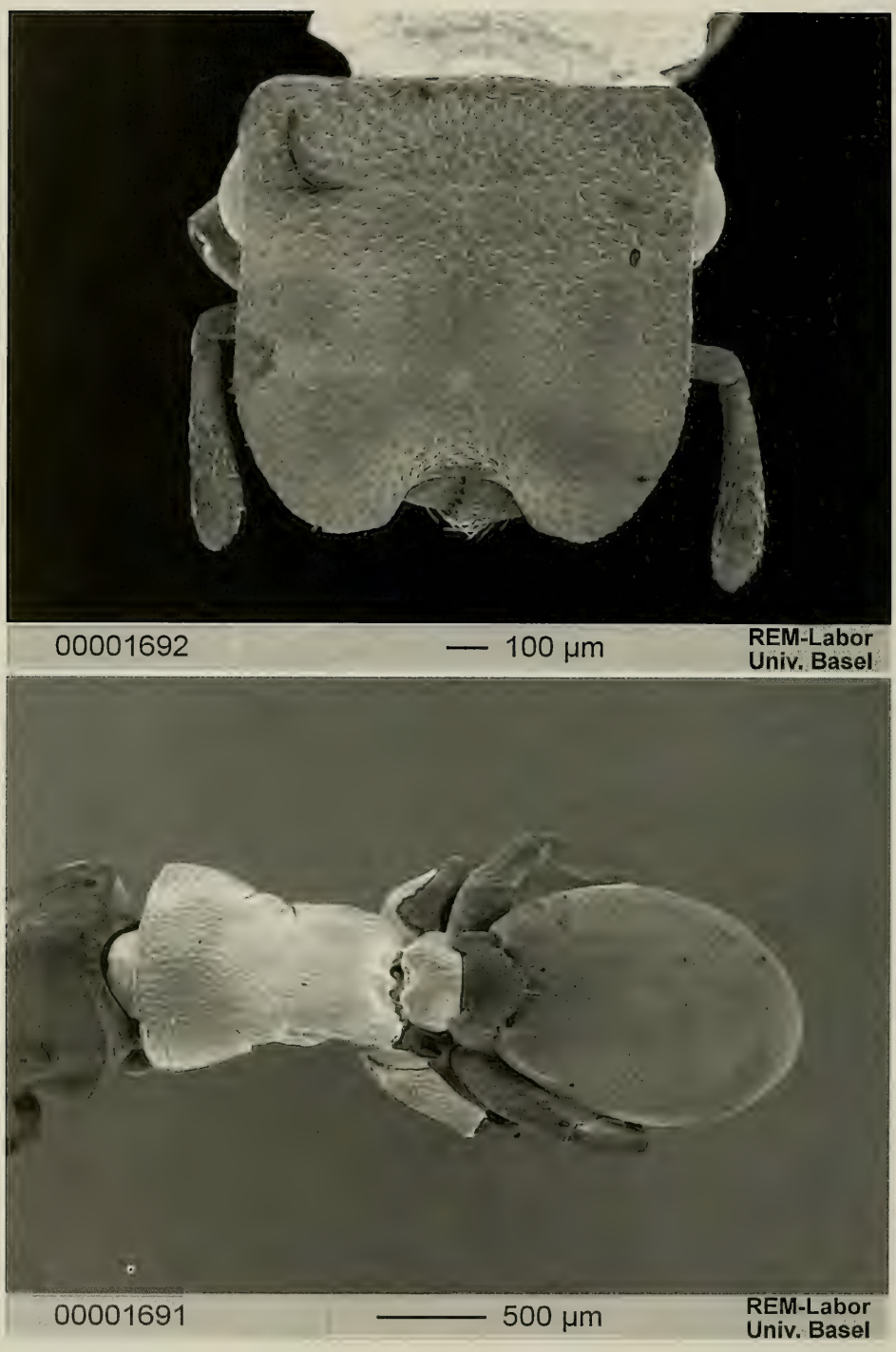


Fig. 192. *Cephalotes incertus* (EMERY). Worker from Mato Grosso, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

holds true for the thoracic dorsum and the dorsum of the postpetiole; gular face of head, sides of thorax (except catepisternum of mesonotum), legs, postpetiole and gaster without distinct foveolae. All foveolae contain golden, canaliculate, appressed scales, which are also present on gular face of head, on sides of mesonotum and on legs, less conspicuous and smaller on gaster. No short, blunt hairs projecting laterally from beneath the rim of the cephalic disc."

Measurements (in mm) and indices: TL 4.84–5.44; HL 1.04–1.16; HW 1.24–1.32; EL 0.24–0.26; PW 1.24–1.32; PeW 0.49–0.53; PpW 0.53–0.57; HBaL 0.31–0.33; HBaW 0.11–0.12; CI 113.8–119.2; PI 100.0; PPeI 249.0–253.1; PPpI 213.6–234.0; HBaI 35.5–36.4.

Gyne (description of KEMPF, 1952). - „Length 6.1 mm. Median head length 1.20 mm. Weber's length of thorax 1.68 mm. Subopaque. Ferruginous. Disc of head with reddish tinge, frontal carinae, membranaceous border of pronotum and epinotum, lateral projections of petiole lighter, with yellowish or lurid hues. Mandibles, funicular segments and tarsi erruginous.

Head subquadrate, the maximum length slightly exceeding the interocular width. Mandibles finely punctured, except the chewing border, which is smooth and shiny, with four distinct teeth toward apex. Supramandibular excision about twice as broad as deep. Clypeus vestigial, elongate. Frontal carinae prolonged caudad above eyes in the form of a very slightly raised carina, which bends obliquely mesad behind the eyes in order to join with the transverse crest of the vertex. Head disc somewhat convex. Ocelli small, amber in color. The median ocellus somewhat larger than the lateral ones. Occipital corners flattened, rounded and crested. A crest, rising shortly behind the posterior condyle of the mandible runs backwards beneath the eye to the occipital corner. Funicular segments 2–8 much broader than long. Penultimate funicular segment conspicuously longer than the preceding segment. Integument finely reticulate-punctate with sparse, large and somewhat elongate squamiferous foveolae, shallow and very sparse on anterior half of cephalic disc, larger, more deeply impressed and crowded, toward the occiput. Cheeks very densely foveolate rugose with crowded scales. All scales are decumbent and silvery.

Thorax longer than broad across the pronotum. The latter sharply marginate anteriorly and laterally; the anterior border transverse and almost straight, the lateral borders subparallel and crested, the shoulders rounded. Transverse pronotal carina absent. Scutum broader than long and flat. Thorax distinctly constricted in front of the epinotum. Basal face of epinotum transversely convex, half as broad as maximum length of thorax; its lateral borders being crested and its posterior corners having a blunt short tooth. Declivous face at right angle to basal face, with a lateral crest arising from beneath the posterior teeth of the basal face. Dorsum of thorax and mesopleura finely reticulate-punctate with sparse, squamiferous foveolae, less conspicuous than those on the cephalic disc. Laterotergites of pronotum and sides of epinotum shagreened, without scales. Declivous face finely punctate and perpendicularly striolated. Femora fusiform, without a distinct angle near the middle of the upper face.

Petiole broader than long; each side with a projecting lobe, which is continuous anteriorly with the anterior border of the petiole, but distinctly set off posteriorly. Anterior face of petiole perpendicularly excavated; dorsum transversely convex. Postpetiole wider than petiole, wider than long. Lateral lobes as in worker, but not quite membranaceous. Dorsum and sides of perpendicular segments sculptured as thorax, with appressed scales.

Gaster elongate, nearly twice as long as broad, with subparallel sides. Anterolateral lobes angulate mesially, not distinctly crested. Finely shagreened, without conspicuous foveolae, but with sparse, short, minute, appressed, silvery scales. Sternites and terminal tergites of gaster with sparse, short and erect setae."

Measurements (in mm) and indices: TL 5.28; HL 1.08; HW 1.22; EL 0.24; PW 1.08; PeW 0.51; PpW 0.58; HBaL 0.32; HBaW 0.12; CI 113.0; PI 113.0; PPeI 211.8; PPpI 186.2; HBaI 37.5.

Material examined. - **Brazil**: Mato Grosso: Poconé, 22.IV.1972, 41 workers, 1 soldier, R. N. WILLIAMS [MZSP]; Santo Antonio de Leverger, 22.XII.1984, 12 workers, 2 soldiers, J. C. TRAGER [MZSP]. Mato Grosso do Sul: Corumbá, 18.X.1953, 3 workers, C. R. GONÇALVES [MZSP]. Rio Grande do Sul: São Leopoldo, 23.VII.1996, 12 workers, E. DIEHL FLEIG [MZSP].

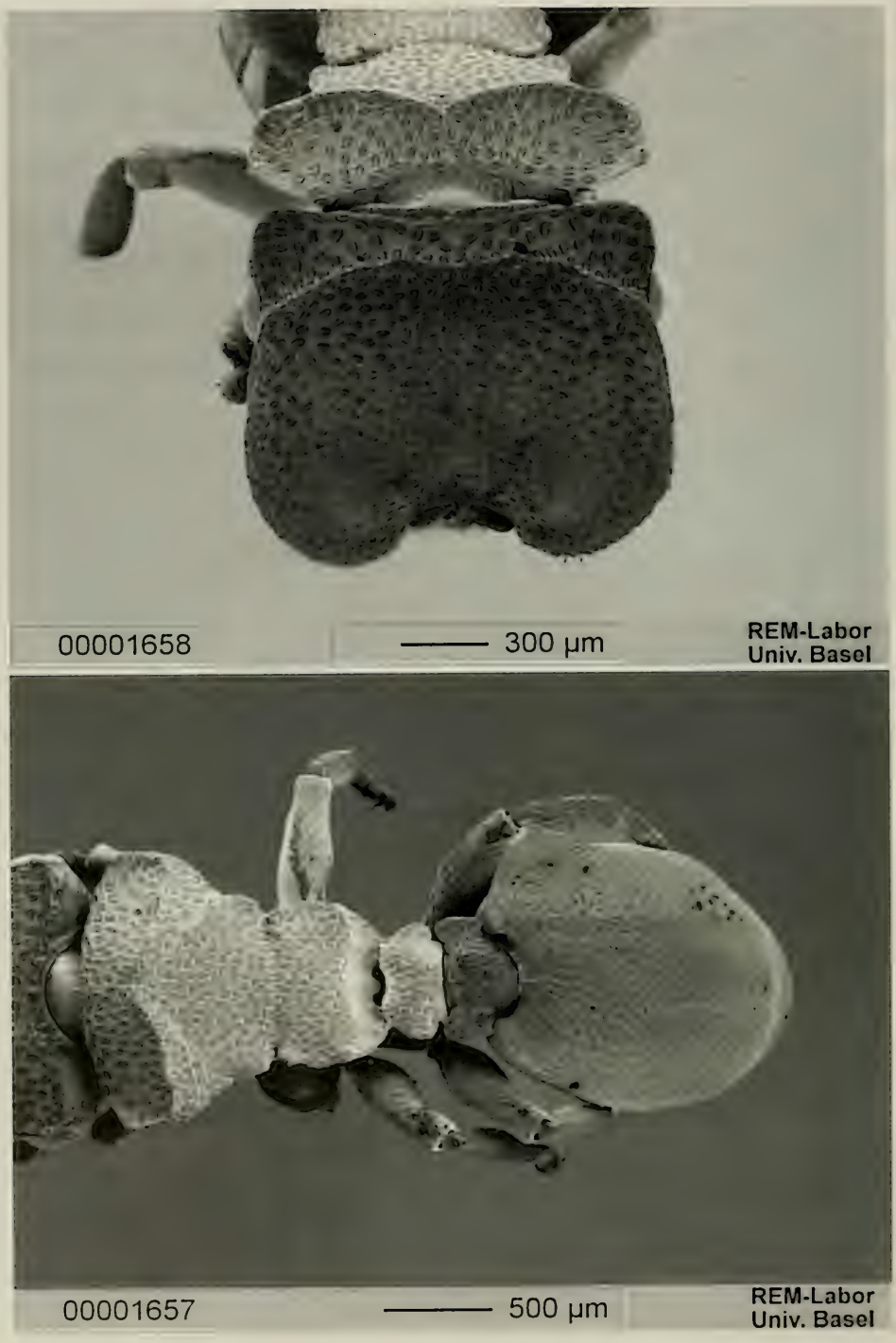


Fig. 193. *Cephalotes incertus* (EMERY). Soldier from Mato Grosso, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Paraguay: N e e m b u c ú : Pilar, 18.X.1982, 2 workers, J. L. PERRET [MHNG].
Argentina: C o r r i e n t e s : Corrientes, 15.VI.1900, 1 worker (holotype) [MCSN]; San Roque, II.1920, 4 workers, J. BOSQ. [MHNG, NHMB]; San Roque, 3 workers, C. BRUCH [MZSP]. S a n t a F é : Fives Lille, 6 workers, WEISER [NHMB, MZSP]; Ceibalito, 7 workers, 1 gyne [MZSP]. E n t r e R í o s : Hernandarias, 07.VI.1951, 2 workers [MZSP].

D i s c u s s i o n . - This is the species with the lightest body colour within the clade, a condition rendering the characteristic maculation of the gaster less visible than in other, related species. One of the Argentinean workers from Ceibalito has the medial part of the gaster entirely black.

D i s t r i b u t i o n : Brazil, Argentina, Paraguay.

5.6.12. The *grandinosus* clade

This clade contains a small set of seven species characterised by a unique but important synapomorphy: the hind femora of the soldier with a dorsal crest. Only the nominal species *grandinosus* has a broad geographical distribution; other members of the clade appear to be restricted to the Brazilian-Peruvian rain forests and two species are fossil in Dominican amber. The Recent species of this clade are also among the minority of *Cephalotes* with light colours. The coloration, of course, can not be assessed with certainty for the fossils.

Species included in the clade: *foliaceus*, *grandinosus*, *klugi*, *maya*, *olmecus*, *persimilis*, *persimplex*.

† *Cephalotes olmecus* DE ANDRADE new species
Figs. 15 A & B, 194, 195

T y p e m a t e r i a l : holotype worker from the Mexican amber sample Mex. 1 and paratype small soldier from the Mexican amber sample H 10–201, both in the GOPC.

D e r i v a t i o n o m i n i s : this species is named after the Olmecs, one of the ancient peoples of Mexico.

D i a g n o s i s . - A member of the *grandinosus* clade differing from all the other species of the clade in the worker by the presence of a narrow, crenulate crest on the dorsum of the fore femora, and in the soldier by the strongly crenulate carinae on the dorsum of the fore femora.

W o r k e r (Fig. 194). - Head broader than long. Frontal carinae weakly and minutely crenulate. Vertexal angles broad, round and membranaceous. Vertexal margin concave. Mandibles with lateral carina. Antennal club two jointed.

Mesosoma. Scapular angles absent or not visible in dorsal view. Anterior pronotal border straight; pronotal sides with a broad, membranaceous expansion, anteriorly subround and narrowing posteriorly. Promesonotal suture absent. Mesonotal sides with a pair of triangular, membranaceous teeth. Propodeal suture deeply impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous faces of the propodeum with a broad membranaceous expansion originating cranially on the basal face and broadening backwards; margin of the membranaceous expansion of the propodeum minutely and superficially crenulate.

Petiole with the anterior face truncate; sides of the petiole with a broad, round, wing-shaped, membranaceous expansion directed laterally. Postpetiole with a comparably broad, wing-shaped, membranaceous expansion with round apex and directed forwards.

Gaster suboval and with broad, anterolateral, membranaceous expansions not surpassing the stigma backwards.

Mid and hind femora angulate and with two membranaceous crests on the two distal thirds, one on the dorsal face and another on the ventral face; fore femora with a short dorsal crest. Mid and hind basitarsi with flat and broad base.

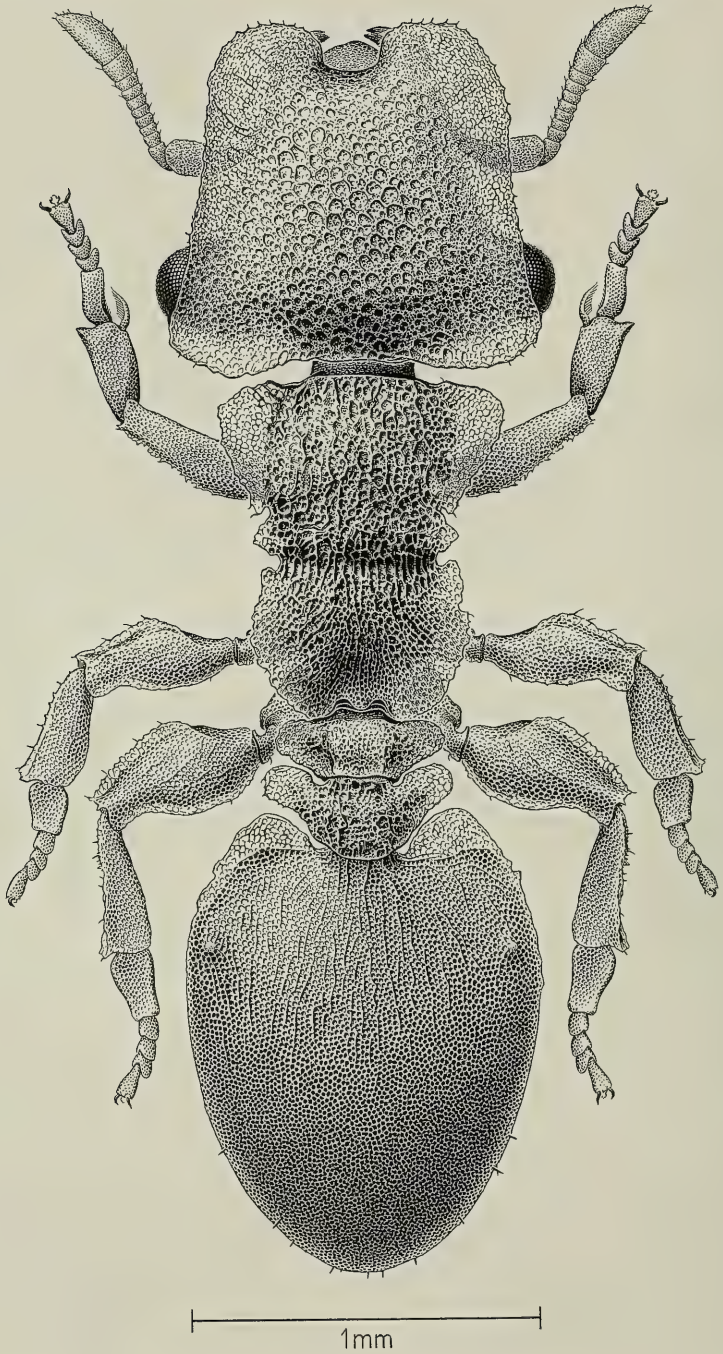


Fig. 194. *Cephalotes olmecus* DE ANDRADE from Mexican amber. Worker in dorsal view.

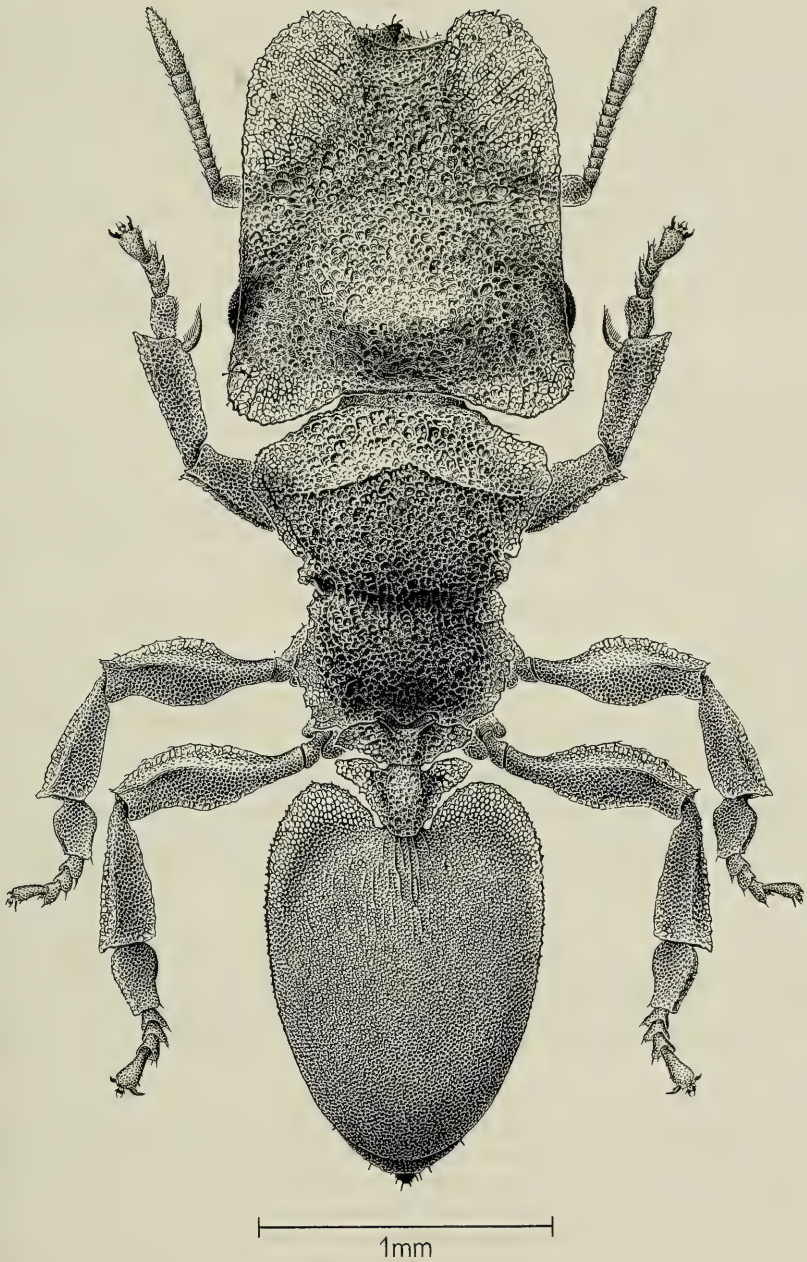


Fig. 195. *Cephalotes olmecus* DE ANDRADE from Mexican amber. Small soldier in dorsal view. Reconstruction by ARMIN CORAY. See Chapter 2 (Material examined) for the preservation conditions of the specimen. The reconstruction presented here implies the interpretation of different body parts as follows. Head made symmetric and reconstruction of small missing parts copied from the opposite side; minor, arbitrary, extension of the observed microsculpture over non-visible parts. Antennae drawn essentially after the right antenna; terminal funicular joints drawn

Sculpture. Head dorsum, mesosoma and pedicel minutely reticulate and foveolate, the foveae larger and more regular on the frons, very irregular on the mesosoma, small on the propodeum and on the pedicel. Pronotum and mesonotum with short rugosities between the foveae. First gastral tergite and legs strongly reticulate, the same type of sculpture but more superficial on the first gastral sternite. Anterior half of the first gastral tergite with thin, longitudinal rugosities

Pilosity. Some fovea with a recurved hair. Sides of the frontal carinae, border of the mesosomal and of the peduncular expansions, and legs with short hairs.

Colour. Light brown. Frontal carinae, vertexal angles and membranaceous expansions light ferruginous and semitransparent.

Measurements (in mm) and indices: TL 3.60; HL 0.83; HW 1.07; EL 0.22; PW 0.82; PeW 0.47; PpW 0.53; HBaL 0.20; HBaW 0.12; CI 128.9; PI 130.5; PPeI 174.5; PPpI 154.7; HBaI 60.0.

S o l d i e r (Fig. 195) (drawing and description based on a small specimen). - Differing from the worker in the following characters: head about as longer as broad. Traces of cephalic disc. Eyes partially hidden by the frontal carinae. Anterior pronotal border convex; pronotal sides with a membranaceous expansion much smaller than in the worker, slender, anteriorly truncate and narrowing posteriorly. Pronotal carina low. Mesonotal sides with a pair of truncate, membranaceous teeth. Anterior face of the petiole concave and dorsally bicarinate. Membranaceous expansions of the petiole and postpetiole with slightly pointed apices. Gaster narrower and with broad, anterolateral, membranaceous expansions surpassing the stigma posteriorly

Hind femora with dorsal membranaceous crest only; fore femora dorsally with a strongly crenulate carina.

Sculpture. Head dorsum, mesosoma and peduncular segments reticulate and with small and irregular foveae. The rest as in the worker.

Pilosity as in the worker but with thicker hairs on the sides of the frontal carinae.

Colour similar to the one of the worker but darker.

Measurements (in mm) and indices: TL 4.26 HL 1.18; HW 1.16; EL 0.18; PW 1.04; PeW 0.46; PpW 0.46; HBaL 0.24; HBaW 0.16; CI 98.3; PI 115.5; PPeI 226.1; PPpI 226.1; HBaI 66.7.

M a t e r i a l e x a m i n e d . - **Mexican amber**: 1 worker, holotype, (reference number: Mex. 1) and 1 dwarf soldier, paratype, (reference number H 10–201), both in the GOPC.

D i s c u s s i o n . - *C. olmecus* appears as the outgroup of a small subclade containing only the Mexican fossil *maya* and the Recent *foliaceus*. *C. olmecus* shares synapomorphically with *maya* and *foliaceus* the highest worker HBaI of the whole genus. Nonetheless, *olmecus* can be immediately differentiated from both ingroup

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and slightly modified from the left antenna. Pronotum and propodeum only slightly modified in contour to correct deformation; microsculpture largely extended to non-visible parts from the few visible ones. Petiole: only the microsculpture of the center copied from the external parts. Postpetiole: contour and part of the sculpture drawn as visible from the ventral side. Gaster: median compression not drawn, right side slightly reconstructed after the left one; microsculpture locally slightly reconstructed; right anterolateral lamella drawn in part from the ventral view. Forelegs: femora drawn after the right leg with correction of the compression; tibiae drawn after the right leg without significant changes; spurs partly reconstructed; tarsomere 1 from the left leg; tarsomeres 2–5 from the right leg. Midlegs: outline of femora wholly reconstructed, only the sculpture drawn as in the specimen; tibiae and tarsi drawn from the right side without significant modifications. Hindlegs: femora partly reconstructed with parts of the opposite one; tibiae from the right leg; tarsi from the left leg.

species by the unique presence of a narrow, crenulate crest on the dorsum of the fore femora of the worker and a strong crenulate carina on the dorsum of the fore femora of the soldier.

We are quite confident in the attribution of the small soldier H–10–201 to the same species as the worker Mex. 1 because of their great similarities in the above unique characters. The different extension of the membranaceous expansions in the two castes reflects, in fact, the differences that one would expect as purely caste-dependant. The exact development of these extensions in the two castes, however, remains unparalleled by most other Recent species.

Distribution: Mexican amber.

† *Cephalotes maya* DE ANDRADE new species
Fig. 196

Type material: holotype worker from the Mexican amber sample Mex. 2.1 in the GOPC.

Derivatio nominis: this species is named after the Mayas, the former rulers of the area of Simojovel, the locality from which the Mexican amber originates.

Diagnosis. - A member of the *grandinosus* clade differing from its sister species, *foliaceus*, in the worker by the first gastral tergite not surrounded by a membranaceous border.

Worker (Fig. 196). - Head broader than long. Frontal carinae minutely crenulate. Vertexal angles broad, round and membranaceous. Vertexal margin concave. Mandibles with lateral carina. Antennal club two jointed.

Mesosoma. Scapular angles absent or not visible in dorsal view. Anterior pronotal border convex; pronotal sides with a broad, membranaceous expansion, anteriorly obtuse and narrowing posteriorly. Promesonotal suture absent. Mesonotum with a pair of broad, round, membranaceous, lateral teeth. Propodeal suture impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous propodeal faces with a broad membranaceous expansion originating from the anterior part of the basal face, projected anteriorly and broadening backwards; margin of the membranaceous expansion of the mesosoma superficially crenulate.

Petiole anteriorly concave; petiolar sides with a broad, wing-shaped, round, membranaceous expansion. Postpetiole also with broad, wing-shaped, membranaceous expansion with round apex and directed forwards.

Gaster suboval and with broad, anterolateral, membranaceous expansions largely surpassing the anterior half posteriorly.

Mid and hind femora angulate; mid and hind femora with two membranaceous crests on the two distal thirds, one on the dorsal face and another on the ventral face; fore femora with a short ventral crest. Mid and hind basitarsi with flat and extremely broad base.

Sculpture. Head dorsum and mesosoma minutely reticulate, with dense and slightly irregular foveae. Peduncular segments with small foveae. Gaster and legs reticulate; first gastral tergite with few, thin, irregular, superficial, longitudinal rugosities.

Pilosity. Some foveae with an appressed hair.

Colour. Body light brown. Frontal carinae, vertexal angles and membranaceous expansions light ferruginous and semitransparent.

Measurements (in mm) and indices: TL 3.78; HL 0.80; HW 1.10; EL 0.17; PW 1.00; PeW 0.48; PpW 0.48; HBaL 0.26; HBaW 0.16; CI 137.5; PI 110.0; PPeI 208.3; PPpI 208.3; HBaI 61.5.

Material examined. - **Mexican amber**: 1 worker, holotype, (reference number: Mex. 2.1) in the GOPC.

Fig. 196. *Cephalotes maya* DE ANDRADE from Mexican amber. Worker in dorsal view. Appendages omitted.

D i s c u s s i o n . - *C. maya* is the sister species of the Recent *foliaceus*. Both species are easily distinguished from others by the fore femora with a broad ventral crest. *C. maya* differs from *foliaceus* by the shorter expansions surrounding the first gastral tergite. *Maya* is, after the Recent *foliaceus*, the species with the second broadest membranaceous expansions of the gaster in the clade.

D i s t r i b u t i o n : Mexican amber.

Cephalotes foliaceus (EMERY) new combination
Figs. 197, 389

Cryptocerus foliaceus EMERY, 1905:172 (footnote). Worker. Original description. Type locality: Pachitea River, Peru. Type material: one worker labelled „Peru, Pachitea, Stdg" [MCSN], examined.

Paracryptocerus foliaceus (EMERY), KEMPF, 1952: 7. Worker and soldier. First combination in *Paracryptocerus*.

Zacryptocerus foliaceus (EMERY), HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *grandinosus* clade differing from all the other species of the clade in the worker and soldier by the first gastral tergite surrounded by a membranaceous border.

W o r k e r (Figs. 197, 389) (description of KEMPF, 1952). - „Length 4.2 mm. Median head length 1.07 mm. Weber's length of thorax 1.12 mm. Yellowish-brown, the anterior portion of the first gastral tergite much paler. Membranaceous borders and frontal carinae yellowish-white.

Head longer than thorax (52:46), broader than long (59:52), convex discally above. Supramandibular excision broad, subrectangular. Borders of frontal carinae and occipital corners finely denticulate. Lateral border of head slightly concave, scarcely upturned above eyes. Occipital corners rounded and membranaceous. Greatest diameter of eyes about 1/5 of maximum head length (11:52).

Thorax, in dorsal view, subquadrate, depressed; sides parallel. Anterior corners of pronotum obtusely angulate, posterior corners rounded. Mesonotum with a broad, apically truncate, membranaceous plate on each side. Mesoepinotal suture distinct laterad, obsolete mesally. Epinotum as wide as pronotum, both with broad membranaceous border. Declivous face not differentiated from the basal face. Femora with a strong longitudinal membranaceous crest apically above and below.

Petiole slightly wider than postpetiole, not impressed anteromesally, without distinctly truncate anterior face above the thoracic insertion, the lateral membranaceous expansions containing a solid recurved spine.

Gaster subcircular, about as wide as long. First gastric tergite surrounded by a broad circular membranaceous border, interrupted only at the postpetiolar insertion.

Head and thorax somewhat shiny; the gaster and appendages subopaque, finely shagreened. Dorsum of head and thorax with squamiferous foveolae. Gaster without conspicuous foveolae. Scales short, rounded and canaliculate. No erect setae on first gastral tergite."

Measurements (in mm) and indices: TL 4.52–4.88; HL 1.10–1.14; HW 1.62–1.68; EL 0.28; PW 1.24–1.32; PeW 0.88–0.97; PpW 0.84–0.93; HBaL 0.31; HBaW 0.19; CI 147.3–147.4; PI 127.3–130.6; PPeI 136.1–141.0; PPpI 141.0–147.6; HBaI 61.3.

S o l d i e r (description of KEMPF, 1952). - „Length 5.0 mm. Median head length 1.27 mm. Weber's length of thorax 1.44 mm. Ferruginous-yellow. Funicular segments 2–9, tarsi, basal end of femora ferruginous. Anterior portion of pronotum, first gastral tergite, except a large circular ferruginous-yellow central area, pale orange to creamy. Marginal foliaceous crests glassy, semitransparent, dark orange around cephalic disc, paler on thorax and femora, almost colorless around gaster.

Head broader than long (80:63), surmounted by an elliptical, excavated disc, the borders of which are subperpendicularly upturned, having two vestigial denticules projecting from the mesal portion above occiput. Supramandibular excision about twice as broad as deep. Apical part of mandibles deflected downward, forming a distinct angle, visible from above as a crest running obliquely across the mandibles. Center of cephalic disc with a median convexity having a pair of antero-lateral extensions and a single postero-median branch. Postero-lateral portion of disc excavate and concave. Occipital lobes crested and obliquely truncate. Antennal scrobes ventral in position; part of cephalic disc above it semitransparent and membranaceous.

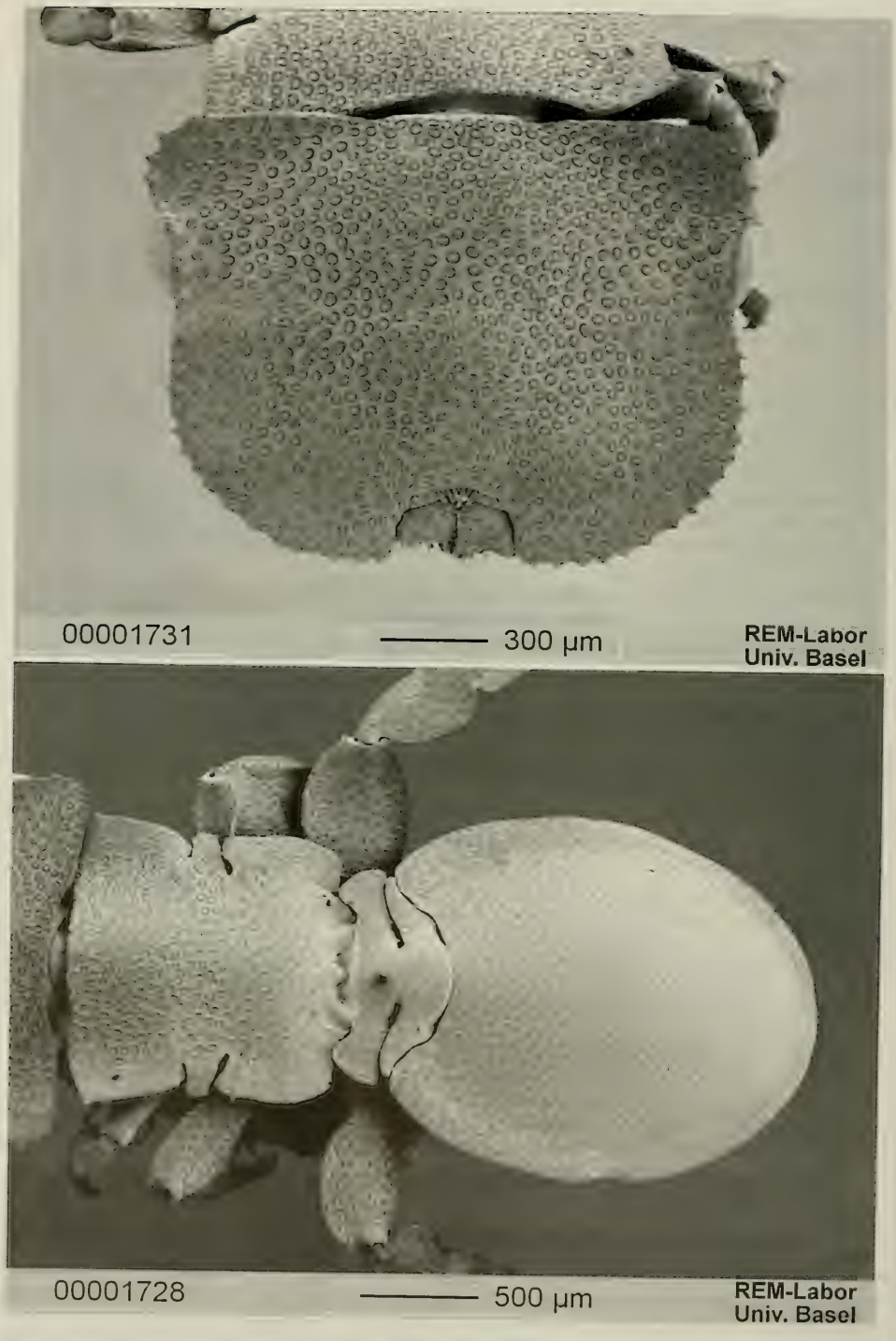


Fig. 197. *Cephalotes foliaceus* (EMERY). Worker from Cavinas (Beni), Bolivia: head (top) and meso- and metasoma (bottom) in dorsal view.

Thorax broader than long (69:56), with marginal membranaceous crests. Transverse pronotal carina strongly crested, interrupted mesally. Promesonotal suture obsolescent mesally. Sides of mesonotum with flattened, rounded and crested lobe. Mesoepinotal suture distinct. Epinotum broader than mesonotum, longitudinally convex with scarcely differentiated basal and declivous faces. A solid upturned tooth on each posterior corner of the basal face. Femora compressed, the apical half with a conspicuous dorsal and ventral crest. Tibiae short and stout, about twice as long as broad. Tarsi very short, the first and fifth segments less than twice as long as broad, segments 2–4 broader than long.

Petiole with a recurve and slender spine on each side, contained within the broad membranaceous border. Anterior and dorsal face of petiole continuously curved in profile. Postpetiole with a foliaceous spine on each side, projecting laterad and slightly cephalad.

Gaster subcircular, the median length subequal to the maximum width (67:69); excised antero-mesially, the remaining margin of the first tergite with a continuous membranaceous border.

Horizontal part of mandibles finely shagreened, deflected portions coarsely rugulose. Head except the excavated part of the disc, coarsely reticulate-rugose. Excavation smooth along the margins, finely reticulate-punctate in the center, with large, sparse, rounded, squamiferous foveolae. Dorsum of thorax and peduncular segments similarly sculptured, the foveolae being somewhat denser and the intervals almost smooth and shiny. Sides of thorax finely reticulate-striated. Appendages finely reticulate-punctate. Dorsum of gaster reticulate-punctate, the squamiferous foveolae very small, shallow, and vestigial."

Measurements (in mm) and indices: TL 3.24 (without postpetiole and gaster missing in the sole known specimen); HL 1.28; HW 1.72; EL 0.28; PW 1.60; PeW 0.96; HBaL 0.32; HBaW 0.19; CI 134.4; PI 107.5; PPeI 166.7; HBaI 59.4.

Material examined. - **Panama**: Barro Colorado, Nature Monument: Gigante Península, 22.VI.1992, fogging, 3 workers, J. E. Tobin [MCZC].

Colombia: Guajira: Dibulla, 5.III.1896, 1 worker, A. Forel [MHNG].

Peru: Pachitea, 1 worker (holotype), Staudinger [MCSN]; Chanchamayo, 800 m, 01.VIII.1939, 2 workers, W. Weyrauch [MZSP].

Bolivia: Beni: Cavinas, I.1921–1922, 3 workers, W. M. Mann, Mulford Biol. Exp. [USNM]; Lago Rogagua, XI.1954, 1 soldier (postpetiole and gaster missing), W. M. Mann [USNM].

Discussion. - *C. foliaceus* bears with *klugi* (known on a single gyne) several, more than superficial, similarities. Since the gyne of *foliaceus* is still unknown and the two species are geographically close, there is the possibility that *foliaceus*, after discovery of the gyne, will become a junior synonym of *klugi*. The main character separating the two, at present, is the worker HBaI, a character obviously unknown in *klugi* but resulting similar to the one of *grandinosus* in our cladogram by simple inference due to the similarity of the gynes of the two species. One should add also that the sole known soldier of *foliaceus* is without gaster, but Kempf (1952) describes it as with a „large circular ferruginous-yellow central area", an unique autapomorphy among *Cephalotes* soldiers which is present in a few gynes but is particularly visible in the one of *klugi*.

Fernández et al. (1996) report this species also from the Colombian state of Magdalena.

Distribution: Panama, Colombia, Peru, Bolivia.

Cephalotes grandinosus (Smith) new combination
Figs. 198, 199, 200

Cryptocerus grandinosus Smith, 1860: 76. Worker. Original description. Type locality: Ega (= Tefé) (Amazonas, Brazil). Type material: holotype worker labelled „59 10" in BMNH, examined.

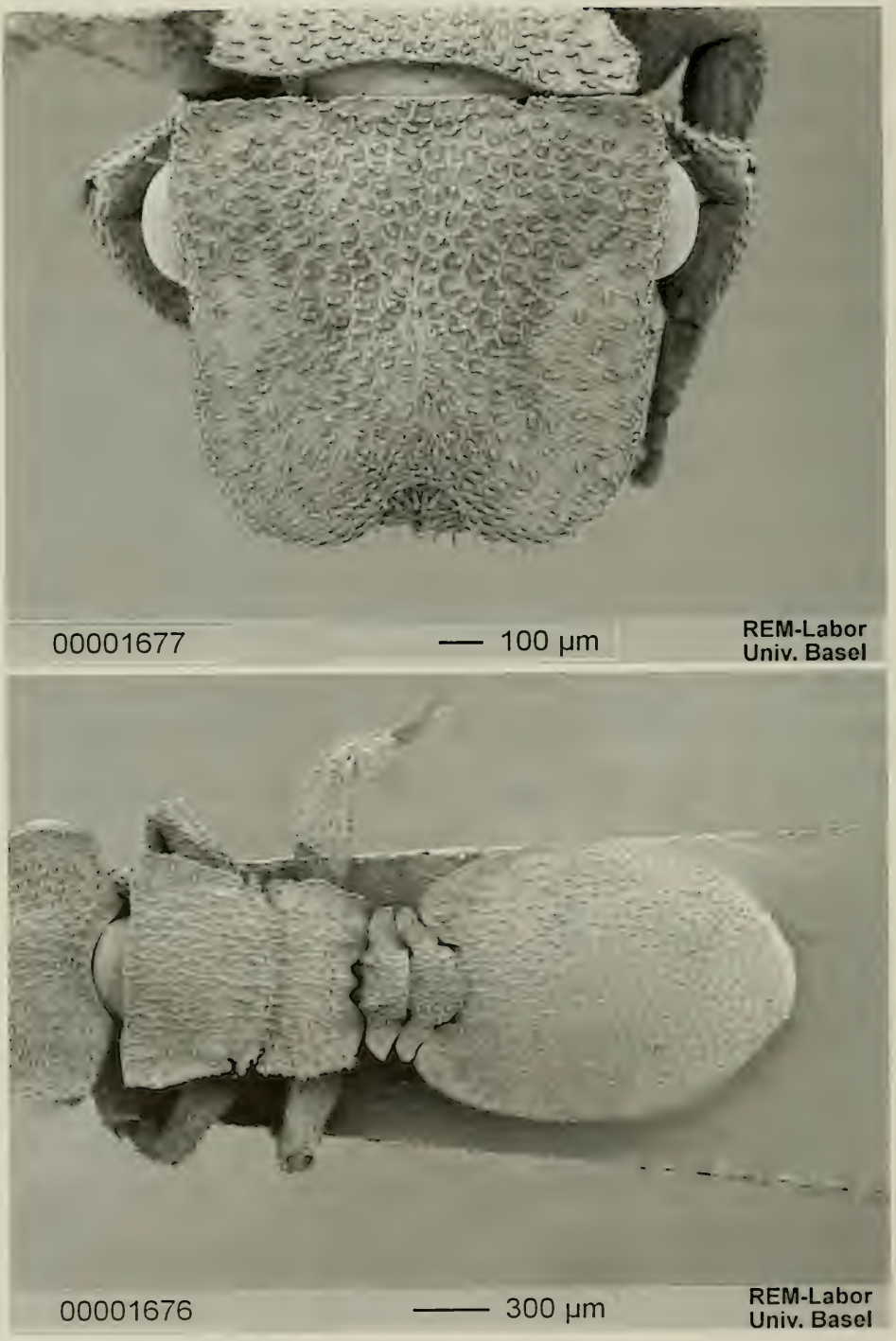


Fig. 198. *Cephalotes grandinosus* (SMITH). Worker from Carimagna (Meta), Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

Cryptocerus grandinosus SMITH, EMERY, 1894 a: 209, pl. 4, figs. 22, 23. Soldier, nec worker nec gyne.

Cryptocerus grandinosus SMITH, FOREL, 1899 a: 50, pl. 3, fig. 12. Worker.

Cryptocerus grandinosus var. *nevadensis* FOREL, 1912: 202. Worker. Original description. Type locality (restricted in the present study): Burithaca (written „Burithaka" by hand of FOREL on the label, not located) (Sierra Nevada de Santa Marta, Colombia), listed first, not Belém (Pará, Brazil), listed second, misidentification. Type material: one syntype worker from Burithaca in MHNG (examined). Synonymy by KEMPF, 1952: 11. The Brazilian syntype from Belém belongs to another species to be described in this paper as *persimilis*.

Paracryptocerus grandinosus (SMITH), KEMPF, 1952: 14. Partim (not page 11 [descriptions of worker, soldier and gyne], not figs. 3 [worker] & 12 [soldier]= *persimilis* and fig. 13 [gyne] = *persimplex*). Only part of the specimens listed belong to true *grandinosus*. First combination in *Paracryptocerus*.

Zacryptocerus grandinosus (SMITH), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *grandinosus* clade characterised in the worker, soldier and gyne by the large and irregular foveae on the head; in the worker only by the flat gastral lamellae and by the mesonotum with two pairs of teeth.

W o r k e r (Fig. 198). - Head subquadrate; frons convex in the middle. Frontal carinae crenulate, covering large part of the mandibles and upturned above the eyes. Vertexal angles membranaceous, with a developed, round margin converging and narrowing before the middle of the vertexal border. Mandibles with a lateral carina visible in side view.

Mesosoma gently convex. Scapular angles absent or not visible in dorsal view. Anterior pronotal border straight; pronotal sides with a broad membranaceous expansion, anteriorly obtuse and narrowing posteriorly. Promesonotal suture superficially impressed in some specimens only. Mesonotum with two pairs of triangular, membranaceous teeth, the anterior pair longer, thicker and broader than the posterior one. Propodeal suture impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous propodeal faces with a broad membranaceous expansion starting from the anterior part of the basal face and strongly projected anteriorly, almost reaching the mesonotal spines forwards and broadening backwards; margin of the membranaceous expansion of the propodeum minutely crenulate and beset with minute hairs.

Petiole with a concave anterior face bearing laterally a pair of obtuse denticles; postpetiolar dorsum sloping anteriorly. Sides of the petiole with a broad, wing-shaped, membranaceous expansion with obtuse tip. Postpetiole slightly convex dorsally; postpetiolar sides with another broad, wing-shaped, membranaceous expansion with obtuse tip.

Gaster oval. First gastral tergite anterolaterally with a broad, flat, membranaceous expansion surpassing the stigma.

Mid and hind femora angulate; hind femora with two membranaceous crests on the two distal thirds, one on the dorsal face and another on the ventral face; mid femora with a narrow membranaceous crest dorsally and with a crest as high as the one on the hind femora ventrally. Mid and hind basitarsi flat and with slightly broad base.

Sculpture. Head dorsum punctate, with dense, large, irregular foveae diminishing in size and less impressed anteriorly. Frontal carinae punctate, with faint, sparse, superficial foveae. Ventral face of the head reticulate and with thin, superficial, longitudinal rugosities. Mesosoma punctate, with irregular foveae superimposed by longitudinal, slightly irregular rugosities. Pedicel with the same type of sculpture as the mesonotum but the foveae smaller and the rugosities thinner. Gaster strongly reticulate and with thin, longitudinal rugosities. Legs reticulate. Membranaceous expansions of mesosoma, pedicel and gaster punctate.

Pilosity. Each fovea with a decumbent hair; similar hairs but not originating from the foveae on the membranaceous expansions of the body. Legs and gaster with appressed hairs slightly thinner than the hairs originating from the foveae, sparser on the sternites. Membranaceous expansions of the propodeum with minute hairs originating from the crenulation. Frontal carinae with sparse, clubbed hairs. Gastral tergites and sternites with

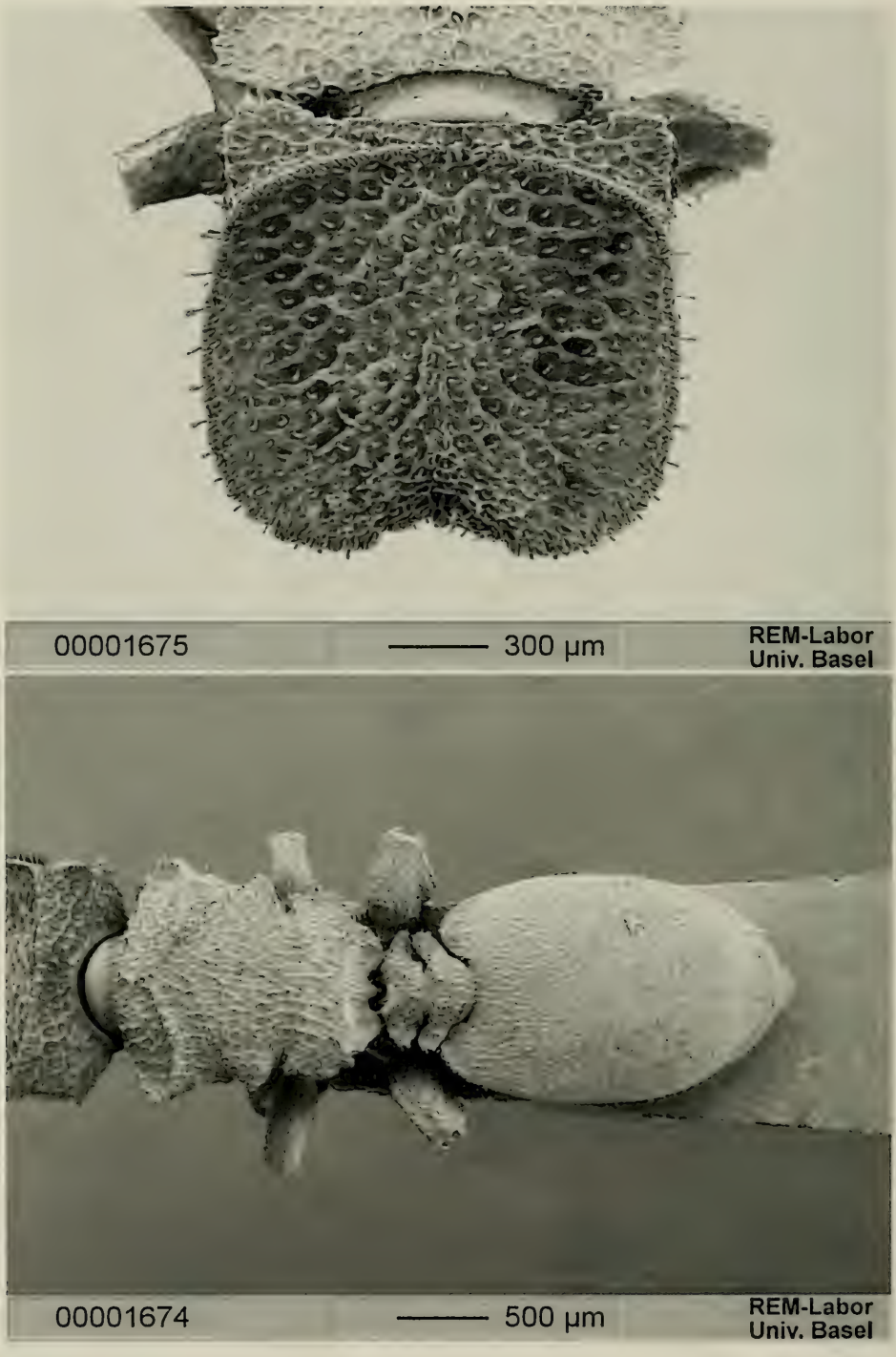


Fig. 199. *Cephalotes grandinosus* (SMITH). Soldier from Carimagna (Meta), Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

slightly clubbed, suberect hairs, denser on the sternites. The gastral sternites bear, in addition, a few long, thin, slightly pointed hairs.

Colour. Body light brown. Frontal carinae opaque, yellow. Membranaceous expansions whitish and semi-transparent. Tarsi brown.

Measurements (in mm) and indices: TL 2.52–4.12 HL 0.66–0.96; HW 0.70–1.10; EL 0.22–0.29; PW 0.60–1.00; PeW 0.37–0.60; PpW 0.37–0.64; HBaL 0.19–0.33; HBaW 0.05–0.11; CI 106.1–116.5; PI 110.0–119.3; PPeI 148.2–166.7; PPpI 148.2–162.2; HBaI 26.3–33.3.

S o l d i e r (Fig. 199). - Head disc subquadrate, with differentiate, strongly crenulate and raised border; sides of the disc gently broadening anteriorly and partially covering the eyes. Posterior border of the disc with a pair of small denticles in some specimens only. Floor of the disc flat to gently convex in the middle. Vertexal angles subround, completely separate from the disc and with marked, crenulate border. Mandibles laterally carinate and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border convex. Humeral angles with an obtuse, membranaceous expansion with the sides gently converging posteriorly up to the middle of the pronotum where it continues into the pronotal carina. Posterior half of the pronotal sides strongly converging. Pronotal carina high, divided in two halves by an incision, each half posteriorly convex and diminishing in height towards the middle of the pronotum. Pronotal suture variably impressed. Promesonotal suture deeply impressed. Mesonotal sides with a pair of broad, triangular, obtuse or pointed teeth followed by a pair of short, thin, pointed, membranaceous denticles. Propodeum with differentiate basal and declivous faces; sides of the basal face with a narrow, crenulate, membranaceous expansion forming cranially a pair of obtuse teeth directed anterolaterally and followed by a convexity converging posteriorly into a pair of small denticles. Declivous face of the propodeum narrowing posteriorly and with membranaceous expansion.

Petiole with concave anterior face; wing-shaped membranaceous expansions with obtuse or pointed tips arise laterally on the two anterior thirds of the petiole. Postpetiole gently convex dorsally, with similar wing-like lateral expansions as the petiole but directed anteriorly and with round tip.

Gaster oval. First gastral tergite anterolaterally with a pair of broad membranaceous expansions not reaching the stigma posteriorly.

Legs as in the worker but with the crest on the dorsal face of the mid and hind femora narrower.

Sculpture. Head dorsum punctate and covered by large, deep, irregular foveae diminishing in size anteriorly. Ventral face of the head reticulate and with superficial foveae denser on the sides. Mesosoma with the same type of sculpture as on the head dorsum, but less deep. Propleurae reticulate and with sparse, broad, superficial foveae. Pedicel and mesopleurae reticulate and with foveae smaller than those on the mesosoma. Declivous face of the propodeum, metapleurae, gaster and legs reticulate. Declivous face of the propodeum, lower metapleurae and anterior third of the first gastral segmental with longitudinal, thin rugae. Center of the first gastral sternite moderately shining.

Pilosity. Each fovea with a suberect clubbed hair. Legs and gaster with appressed, clubbed hairs thinner and shorter than the hairs originating from the foveae, sparser on the sternites. Gaster with erect, short, clubbed hairs, denser on the sternites. Frontal carinae, vertexal angles, mesosoma, pedicel and the border of the tergites and sternites with long, sparse, clubbed hairs. The sternites bear, in addition, a few long, thin, slightly pointed hairs.

Colour. As in the worker.

Measurements (in mm) and indices: TL 5.04–5.44; HL 1.20; HW 1.32–1.36; EL 0.28; PW 1.36; PeW 0.60–0.66; PpW 0.65–0.69; HBaL 0.28–0.30; HBaW 0.11–0.12; CI 110.0–113.3; PI 97.0–100.0; PPeI 206.1–226.7; PPpI 197.1–209.2; HBaI 39.3–40.0.

G y n e (Fig. 200). - Head disc present. Head dorsum gently convex with concave anterolateral sides. Frontal carinae strongly crenulate, expanded anteriorly, converging posteriorly and connected by a slightly convex, crenulate ridge on the vertex. Vertex with a depression reaching the posterior border of the disc. Vertexal angles obtuse and with crenulate

margin. Eyes visible in full dorsal view. Ocelli remote from the posterior border of the disc. Anterior clypeal border concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of small, obtuse, membranaceous teeth converging posteriorly and connected to a narrow pronotal crest. Pronotal sides straight caudally to the angles. Promesonotal suture impressed. Lower mesopleurae with a denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face gently convex and ending in a obtuse or pointed tooth posteriorly; declivous face converging posteriorly and with a narrow membranaceous border on the posterior half.

Petiole with gently concave anterior face; sides of the petiole with a small membranaceous expansion with obtuse or pointed tip. Postpetiole convex dorsally; postpetiolar sides with a broad, round, lateral expansion directed anteriorly.

Gaster. First gastral tergite anterolaterally with a pair of broad lobes with a thin membranaceous expansion not reaching the stigma posteriorly.

Legs as in the soldier but with the dorsal face of the mid femora superficially carinate.

Sculpture and pilosity as in the soldier.

Colour. Light brown. Frontal carinae yellowish-opaque and semitransparent. Tarsi brown. First gastral tergite with a pair of dark brown maculae on the middle of the dorsum, superficially connected medially in some specimens.

Measurements (in mm) and indices: TL 6.96–7.08; HL 1.28–1.32; HW 1.28–1.30; EL 0.32; PW 1.24–1.32; PeW 0.61; PpW 0.68–0.76; HBaL 0.41–0.44; HBaW 0.14; CI 98.5–100.0; PI 98.5–103.2; PPeI 203.3–216.4; PPpI 163.1–194.1; HBaI 31.8–34.1.

Material examined. - **Costa Rica**: 5 km S of Liberia, Guanacaste Prov. 21.VIII.1963, 1 worker, D. H. Janzen [USNM]; Pen. Osa, Par. Nat. Corcovado, Sirena 8°28' N, 83°35' W, 0–100 m, 03.XI.1982, 1 worker, 1 soldier, J. Longino [MCZC].

Panama: Las Cumbres, 23.I.1983, 1 worker, 1 soldier, D. E. Wheeler [MCZC].

Colombia: Magdalena: Burithaca, 1 worker (syntype of var. *nevadensis*), Forel [MHNG]; Río Frío, 21.IX.1926, 1 soldier, G. Salt [MCZC]. Meta: Carimagna, 13.XI.1972, 370 m, 6 workers, 3 soldiers, M. L. Corn [MZSP].

Venezuela: Monagas: Barrancas, R. Orinoco, I & II.1935, 3 workers, 1 soldier, N. A. Weber [MCZC].

Trinidad & Tobago: Trinidad: Port of Spain, 1 soldier, A. Busck [USNM]; St. Augustine, IV.1929, 2 workers, Darlington [MZSP]; St. Augustine, 11.V.1935, 2 workers, 1 gyne, N. A. Weber [MCZC]; Arima Forest Reserve, S of Arima, 12.XII.1934, 2 workers [MCZC]; Northern Range, 25.V.1935, 1 soldier, N. A. Weber [MCZC].

Guyana: Kartabo, VII-VIII.1920, 10 workers, 1 gyne [MCZC]; Bartica, 15–20.IX.1917, 1 worker, Wm. Beebe [MCZC].

Brazil: Amazonas: no further locality, 1 worker, 1 gyne, W. M. Bates [ZSMC]; Tefé, 1 worker (holotype) [BMNH]; Reserva Fl. A. Ducke, 2° 55' S, 59°59' W, terra firme, 26.VIII, 30.IX, 15.X.1982, 3 workers, Adis et al. [INPA]; same locality, 26.I.1996, 1 gyne, M. L. de Andrade [INPA]; Rio Solimões, Ilha de Marchantaria, 59°58' W, 3°15' S, várzea, Lago Central and Lago Camaleão, 02.IX.1982, 3 workers, Adis et al. [INPA]; Ilha de Curari, várzea, 19.II.1976, 1 worker, J. Adis [INPA]. Pará: no further locality, 15 workers, 1 soldier [MCSN]; Primavera, Quatipuru, 27–28.XI.1992, 1 worker, J. Dias [MPEG]; São João de Pirabas, Japerica, 16–18.XII.1992, 2 gynes, J. Dias [MPEG]; Rio Comuná, 1928, 1 soldier, Sampaio [MZSP]; Cachoeira do Breu, X.1928, 1 worker, Sampaio [MZSP]. Rondônia: Vilhena, XI.1973, 1 worker, M. Alvarenga [MZSP]. Bahia: Santo Amaro, ESOMI, 09.III.1988, 3 workers, E. C. Ferraz [CPCC]. Mato Grosso: Utiariti, Rio Papagaio, 325 m, VIII.1961, 2 workers, K. Lenko [MZSP]. Mato Grosso do Sul: Fazenda do Cervo, município de Três Lagoas, 15–18.IX.1964, 1 worker, Exp. Dep. Zool. [MZSP]. São Paulo: Cajuru, 08.II.1964, 2 workers, H. M. Carder [MZSP].

Bolivia: Beni: Riberalta, I.1921–22, 1 gyne, W. M. Mann [USNM].

Discussion. - Previously, under the name *C. grandinosus*, two other species described in this paper as new had been confused. We explain this fact by the

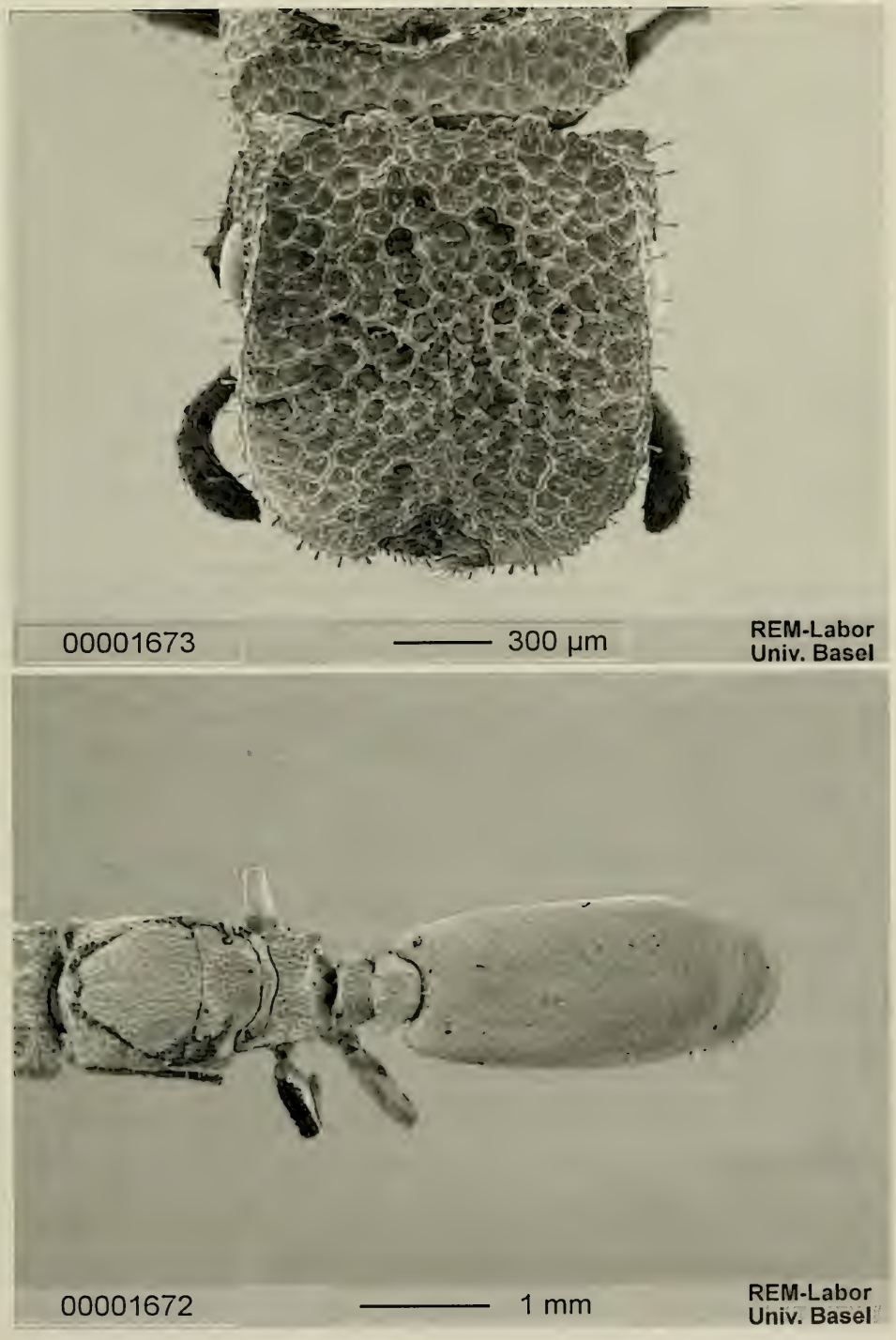


Fig. 200. *Cephalotes grandinosus* (SMITH). Gyne from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

previously availability of limited series, essentially workers not associated with soldiers or gynes, in most collections and by the consequent, forced attempts to associate in a single species material of different castes and of spurious provenance. After examination of a series of workers and soldiers from the same nest and of another nest series including workers and a gyne, the morphological range of this species became clear. The worker, soldier and gyne of *C. grandinosus* are clearly separate from *persimilis* and *persimplex* by the broader and irregular foveae on the head dorsum.

Three workers from the Reserva Ducke (Manaus, INPA) differ from the other workers of *grandinosus* we have been able to examine by the much more crenulate membranaceous expansions of the body. A unique gyne from Amazonas in ZSMC differs from the other gynes of *grandinosus* by the smaller size (6.06 mm vs. 6.96–7.08 mm) and by the more regular foveae on the head dorsum. The soldier mentioned by EMERY (1894) from Pará is a dwarf soldier only 3.90 mm long. We consider nonetheless these specimens as *grandinosus* on the basis of our present understanding of this species.

FERNÁNDEZ et al. (1996) report this species also from the Colombian states of Amazonas, Huila, and Caquetá.

Distribution: Costa Rica, Panama, Colombia, Venezuela, Trinidad, Guyana, Brazil, Bolivia.

Cephalotes klugi (EMERY) new combination

Cryptocerus klugi EMERY, 1894 a: 210, figs. 27, 28. Gyne. Original description. Type locality: Mato Grosso (Brazil). Type material: holotype dealate gyne (unique) labelled: „Brésil, Prov. Matto Grosso, 1886, P. Germain, *Cryptocerus klugi* Emery, Type", examined [MCSN].

Paracryptocerus klugi (EMERY), KEMPF, 1958 a: 139. First combination in *Paracryptocerus*.

Zacryptocerus klugi (EMERY), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *grandinosus* clade characterised in the gyne by the yellow-orange gaster with a dark-brown median, transversal stripe. It differs from its sister species *grandinosus* by the smaller and more superficial body foveolation.

Gyne. - Head disc present. Head dorsum with concave sides and with gently convex frons. Frontal carinae with parallel sides. Posterior border of the disc slightly convex and medially incised by the depression of the vertex. Border of the frontal carinae raised and sparsely crenulate. Vertexal angles obtuse and marginate. Eyes visible in full dorsal view. Ocelli remote from the posterior border of the head disc. Anterior clypeal border concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border straight. Humeral angles with a pair of obtuse, membranaceous borders diverging backwards and connected to a weak pronotal crest shortly interrupted in the middle. Pronotal sides posterior to the angles straight. Promesonotal suture impressed. Lower mesopleurae with a stout denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face convex, ending in a round tooth posteriorly; sides of the declivous face converging posteriorly.

Anterior face of the petiole concave; petiolar dorsum gently sloping anteriorly; petiolar sides with a narrow, convex, lamellaceous expansion. Postpetiole convex; anterior half of its sides with a pair of obtuse teeth directed laterally and with narrow, membranaceous expansions.

Gaster with a pair of obtuse lobes protruding anteriorly and with the margin not reaching the stigma posteriorly.

Legs. Fore coxae angulate anteriorly. Hind femora gently compressed and carinate dorsally; posterior margin of the ventral face of the mid and hind femora with a narrow, membranaceous crest. Hind basitarsi long and flattened at the base.

Sculpture. Frons covered by small, dense, superficial foveae diminishing in size anteriorly: Sides of the head dorsum superficially punctate and with rare foveae. Frontal carinae transparent. Ventral face of the head reticulate and with minute, sparse, shallow foveae. Pronotum medically with the same type of sculpture as on the sides of the head. Mesonotum and scutellum reticulate and with foveae as broad as on the posterior part of the frons, the foveae diminishing in size on the posterior part of the scutellum. Propleurae, lower mesopleurae, metapleurae and declivous face of the propodeum reticulate; few thin, faint rugulae transversally oriented on the declivous face of the propodeum and longitudinal on the metapleurae and on the lower mesopleurae. Posterior part of the pronotum, upper mesopleurae, basal face of the propodeum and pedicel reticulate and with dense, small foveae as on the frons. Gaster and legs reticulate, with thin, faint, longitudinal rugosities on the anterior third of the first gastral tergite.

Pilosity. Each fovea with an appressed hair. Border of the frontal carinae and of the vertexal angles, mesosoma, pedicel and tergites with sparse, suberect, clubbed hairs; similar hairs but shorter on the sternites and on the legs. Gaster and legs with an additional type of hairs, thin, sparse and appressed. Sternites, distally, with rare, long, thin, slightly pointed hairs.

Colour. Head dorsum, anterior half of the ventral part of the head, pronotum, sides of the pedicel, of the basal face of the propodeum, posterior half of the first tergite, two posterior thirds of the sternites and legs light brown; femora darker; clypeus, posterior half of the ventral part of the head, mesonotum, scutellum, propodeum, pedicel, pleurae, second fourth of the first gastral tergite and anterior third of the first gastral sternite black. Anterior fourth of the first gastral tergite yellow.

Measurements (in mm) and indices: TL 7.06; HL 1.28; HW 1.46; EL 0.34; PW 1.48; PeW 0.60; PpW 0.84; HBaL 0.44; HBaW 0.16; CI 114.1; PI 98.6; PPeI 246.7; PPpI 176.2; HBaI 36.4.

Material examined. - **Brazil**: Mato Grosso: no further locality, 1886, 1 gyne (holotype), P. GERMAIN [MCSN].

Discussion. - The gyne of *C. klugi*, in our cladogram, appears as a member of the *grandinosus* clade, since it shares synapomorphically with *grandinosus* the vertexal concavity prolonging backwards to the posterior border of the disc which is incised, a gyne character in our data matrix, though the soldier of *klugi* is still unknown, of course. *Klugi* can be easily differentiated from *grandinosus* in the gyne by the much smaller, shallower and sparser foveae on the head and mesosoma. At the present state of knowledge there seems to be no doubt on the specific status of *klugi*. See also the discussion under *foliaceus*.

Distribution: Brazil.

Cephalotes persimilis DE ANDRADE new species

Figs. 201, 202, 203, 204

Cryptocerus grandinosus (SMITH), EMERY, 1894 a: 209, pl. 4, figs. 24–26 Worker and gyne (nec soldier). Nec SMITH, 1860. Misidentification.

Cryptocerus grandinosus var. *nevadensis* FOREL, 1912: 202. Worker. Partim. Misidentification. Belém (Pará, Brazil), given as second locality for the new variety and not Burithaca (Colombia), type locality of *nevadensis* as restricted in the present study. Misidentification.

Paracryptocerus grandinosus (SMITH), KEMPF, 1952: 11, figs. 3, 12. Partim. Worker and soldier (nec gyne). Nec SMITH, 1860. Misidentification.

Type material: holotype soldier, Tanquinho, Feira de Santana, Bahia, Brazil, 08.XII.1953, C. R. Gonçalves (MZSP); paratypes 1 worker, 1 soldier, same data as the holotype (MZSP).

D e r i v a t i o n o m i n i s : from the Latin *persimilis* = very similar (Cicero), referred to the great similarity between this species and *C. grandinosus*.

D i a g n o s i s . - A member of the *grandinosus* clade differing from its sister species *persimplex*, in the worker and soldier by the body hairs longer and thinner, and, in the gyne, by the frontal carinae crenulate and with denser hairs.

W o r k e r (Fig. 201). - Head subquadrate; frons gently convex. Frontal carinae covering the sides of the mandibles and slightly upturned above the eyes; border of the frontal carinae superficially crenulate. Vertexal angles membranaceous, with an obtuse margin converging and narrowing before the middle of the vertexal border. Mandibles with thick lateral carina.

Mesosoma gently convex. Scapular angles absent or not visible in dorsal view. Anterior pronotal border straight; pronotal sides with a broad, gently concave membranaceous expansion, anteriorly angulate and narrowing posteriorly. Promesonotal suture superficially impressed or absent. Mesonotum with two pairs of triangular, membranaceous teeth, the anterior pair longer, thicker and broader than the posterior one. Propodeal suture impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous propodeal faces with a broad membranaceous expansion starting from the anterior part of the basal face and strongly projected anteriorly, almost reaching the mesonotal spines forwards and broadening backwards.

Petiole with a concave anterior face laterally marked by a small pair of obtuse denticles; petiolar dorsum sloping anteriorly. Sides of the petiole with a broad, gently concave, wing-shaped, membranaceous expansion with round tip. Postpetiole slightly convex dorsally; postpetiolar sides with another broad, wing-shaped, membranaceous expansion with round tip.

Gaster and legs as in *persimplex*.

Sculpture. Head dorsum with dense, small foveae diminishing in size and less impressed anteriorly. Frontal carinae with faint, sparse, superficial foveae and with longitudinal rugosities. Ventral face of the head reticulate and with thin, superficial, longitudinal rugosities. Mesosoma with irregular foveae superimposed by longitudinal, irregular rugosities. Pedicel with the same type of sculpture as on the mesosoma but with smaller foveae. Gaster and legs strongly reticulate; thin, irregular, longitudinal rugosities on the anterior third of the first gastral tergite and on the legs. Membranaceous expansion of mesosoma, pedicel and gaster punctate and with thin, longitudinal rugosities.

Pilosity. Each fovea with a decumbent or an appressed hair; similar hairs but not originating from the foveae on the membranaceous expansions of the body. Legs and gaster with appressed hairs thinner and shorter than the hairs originating from the foveae. Frontal carinae anteriorly and over the eyes, and posterior part of the gastral segments with rare to sparse, clubbed hairs. The gastral sternites bear, in addition, a few long, thin, slightly pointed hairs.

Colour. Body light brown. Frontal carinae opaque, yellow. Membranaceous expansions whitish and semi-transparent. Tarsi brown.

Measurements (in mm) and indices: TL 3.52–4.56; HL 0.83–1.08; HW 0.95–1.24; EL 0.26–0.29; PW 0.87–1.16; PeW 0.56–0.76; PpW 0.55–0.76; HBaL 0.22–0.31; HBaW 0.09–0.15; CI 113.6–115.9; PI 105.6–107.4; PPeI 150.8–160.7; PPpI 149.2–163.6; HBaI 40.0–48.4.

S o l d i e r (Fig. 202). - Head disc subquadrate, with the border differentiate, sparsely and superficially crenulate and raised on the sides only; sides of the disc parallel or broadening anteriorly, covering or not the eyes. Posterior border of the disc with a pair of small denticles. Floor of the disc gently convex in the middle. Vertexal angles obtuse to pointed, completely separate from the disc and with marked, crenulate border. Mandibles laterally carinate and laterally hidden by the frontal carinae.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a short or broad, obtuse, membranaceous expansion with straight sides posteriorly up to the middle of the pronotal sides where it continues into the pronotal carina. Posterior half of the pronotal sides strongly converging. Pronotal carina high, each half posteriorly convex and diminishing in height towards the middle of the pronotum. Pronotal suture impressed. Promesonotal suture deeply impressed. Mesonotal sides with a pair of broad, triangular, obtuse or pointed teeth followed by a pair of thin, pointed, membranaceous denticles. Propodeum with

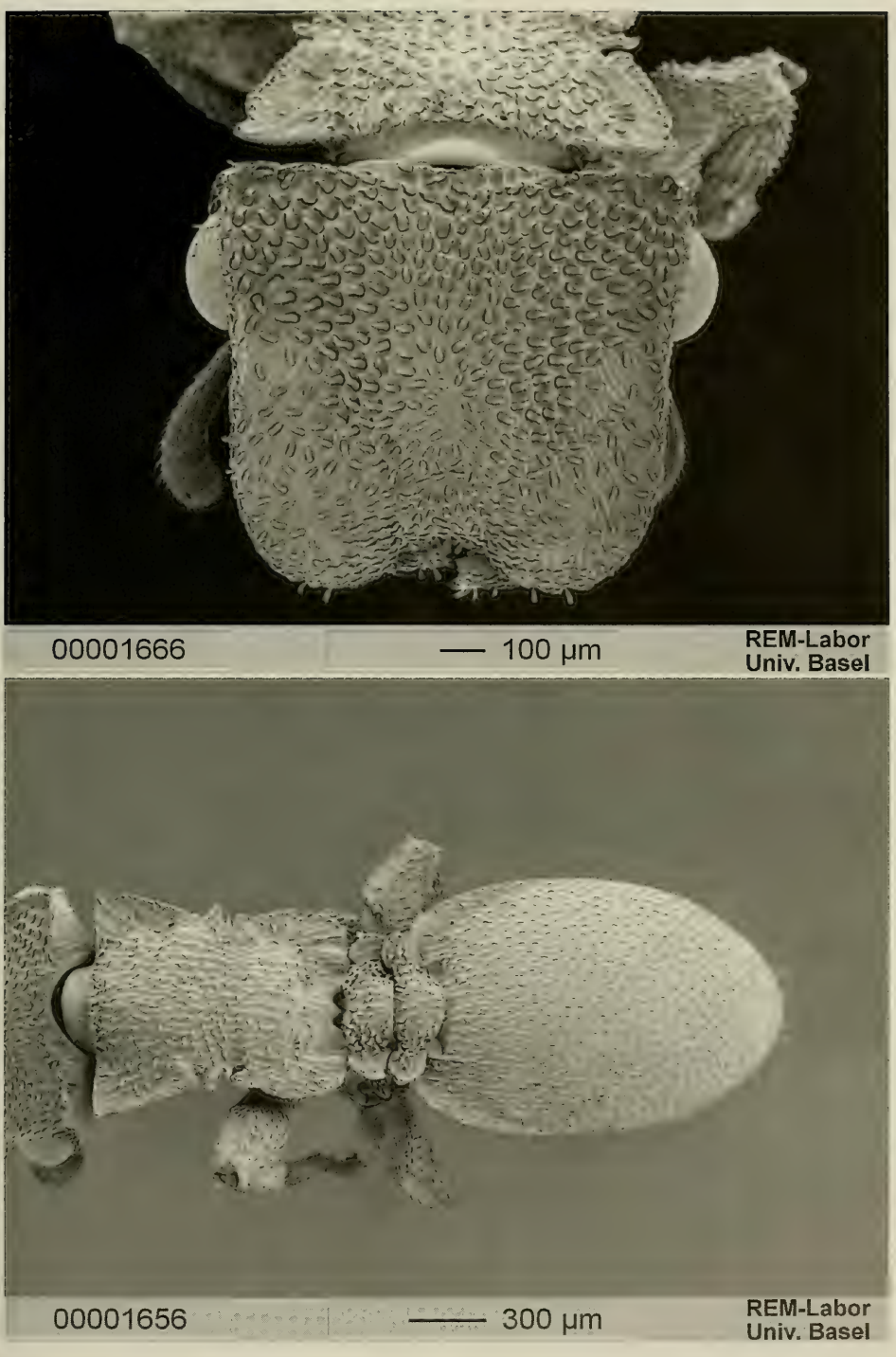


Fig. 201. *Cephalotes persimilis* DE ANDRADE. Worker from Itaberaba (Bahia), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

differentiate basal and declivous faces; sides of the basal face with a narrow, crenulate, membranaceous expansion, forming cranially a pair of obtuse teeth directed anteriorly and followed by a convexity converging posteriorly into a pair of small denticles. Declivous face of the propodeum narrowing posteriorly and with a broad, membranaceous expansion.

Pedicel and legs as in *persimplex*.

Gaster oval, with a pair of lobes protruding anteriorly and bearing narrow membranaceous expansions.

Sculpture. Head dorsum superficially punctate, slightly shining and with foveae with diameter smaller than their interspaces and diminishing in size anteriorly. Ventral face of the head punctate and with anastomosing, superficial foveae denser over the sides. Mesosoma and pedicel with the same type of sculpture as the posterior part of the head dorsum but with denser foveae, the foveae smaller on the propodeum and on the pedicel. Declivous face of the propodeum, gaster and legs reticulate; few longitudinal, thin rugae on the declivous face of the propodeum and on the anterior third of the first gastral segment. Center of the first gastral sternite superficially shining.

Pilosity. Each fovea with an appressed hair. Legs and gaster with appressed hairs thinner and shorter than the hairs originating from the foveae. Frontal carinae, vertexal angles, mesosoma, pedicel with sparse, clubbed hairs; similar hairs but shorter on the gaster. The sternites bear, in addition, a few long, thin, slightly pointed hairs.

Colour. As in the worker.

Measurements (in mm) and indices: TL 4.38–5.60; HL 1.04–1.28; HW 1.22–1.48; EL 0.27–0.32; PW 1.20–1.44; PeW 0.57–0.77; PpW 0.58–0.80; HBaL 0.22–0.33; HBaW 0.12–0.16; CI 115.5–121.4; PI 95.7–104.7; PPeI 185.5–217.5; PPpI 180.0–210.2; HBaI 40.9–48.5.

G y n e (Fig. 203). - Head disc present. Head dorsum convex with gently concave anterolateral sides. Frontal carinae crenulate, expanded anteriorly, converging posteriorly and connected by a slightly convex carina on the vertex. Vertex with a superficial depression between the pair ocelli. Vertexal angles obtuse and with crenulate margin. Eyes visible in full dorsal view. Ocelli remote from the posterior border of the head disc. Anterior clypeal border concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with or without a pair of small, obtuse, membranaceous teeth converging posteriorly and connected with a narrow pronotal carina. Pronotal sides posterior to the angles straight. Promesonotal suture impressed. Lower mesopleurae with a denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face convex and ending in a round tooth posteriorly; declivous face converging posteriorly and with a narrow membranaceous border on the posterior half.

Pedicel, gaster and legs as in *persimplex*.

Sculpture. Head dorsum with dense, deep, round foveae diminishing in size anteriorly. Interspaces between the foveae minutely punctate and shining. Ventral part of the head and propleurae with superficial, irregular, anastomosing foveae, the foveae denser on the ventral sides of the head. Pronotum, propleurae, mesonotum and scutellum minutely reticulate and foveolate, the foveae sparser on the mesonotum and on the propleurae. Basal face of the propodeum, mesopleurae and pedicel superficially reticulate and with dense, small foveae, the foveae rare on the middle of the lower mesopleurae. Declivous face of the propodeum, metapleurae, gaster and legs reticulate; few longitudinal rugosities on the declivous face of the propodeum, on the upper and lower parts of the metapleurae and on the anterior third or anterior half of the first gastral tergite, the latter also with sparse piligerous foveae.

Pilosity. Each fovea with a decumbent or appressed hair. Legs and gaster with appressed hairs slightly thinner than the hairs originating from the foveae, sparser on the sternites. Frontal carinae with sparse, clubbed hairs. Gastral tergites and sternites with slightly clubbed, suberect hairs, denser on the sternites. The gastral sternites bear, in addition, a few long, thin, slightly pointed hairs.

Colour. Light brown. Frontal carinae yellowish-opaque. Tarsi brown. First gastral tergite with a pair of dark brown maculae on the middle of the dorsum faintly connected medially in some specimens.

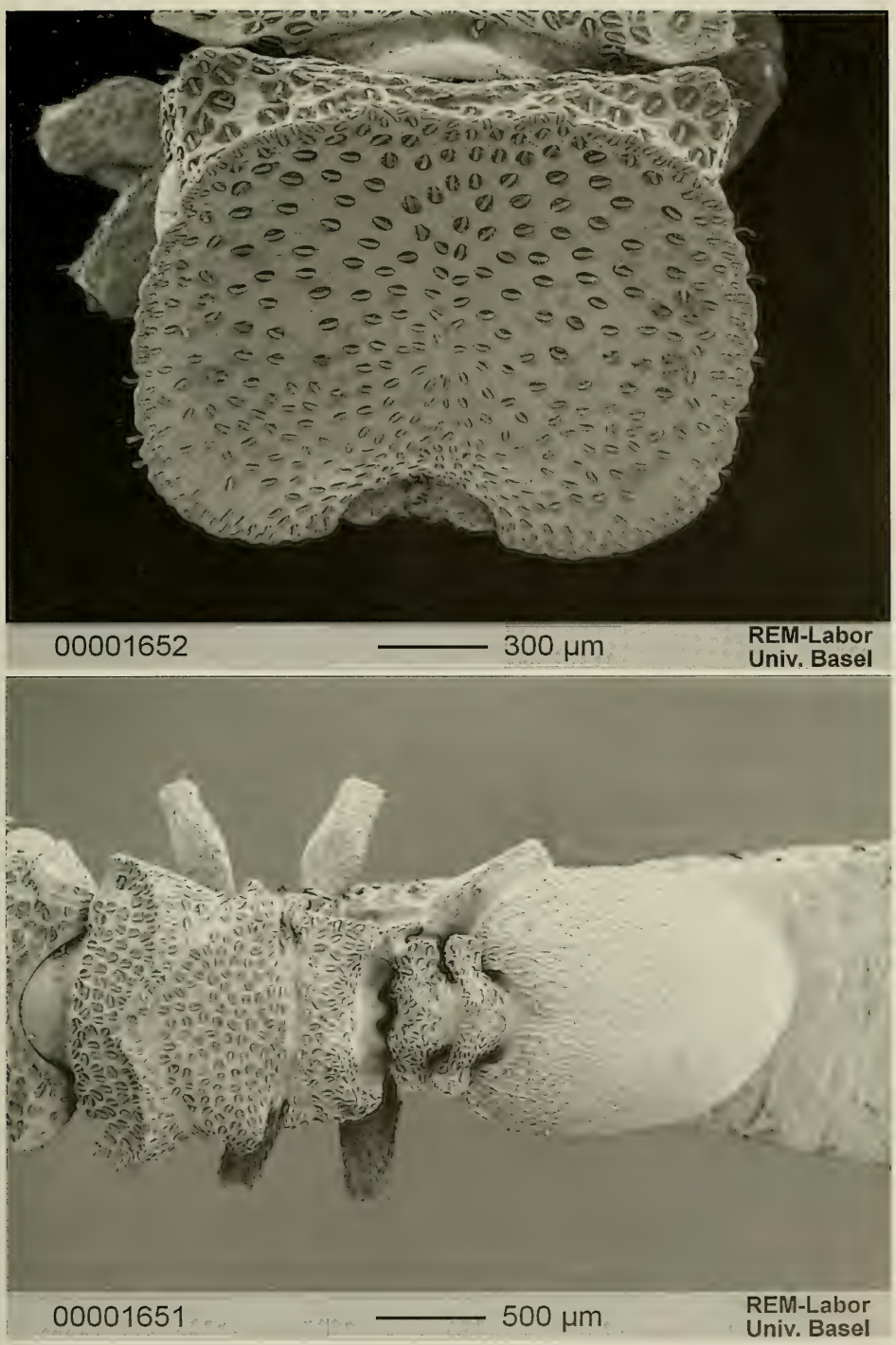


Fig. 202. *Cephalotes persimilis* DE ANDRADE. Soldier from Feira de Santana (Bahia), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

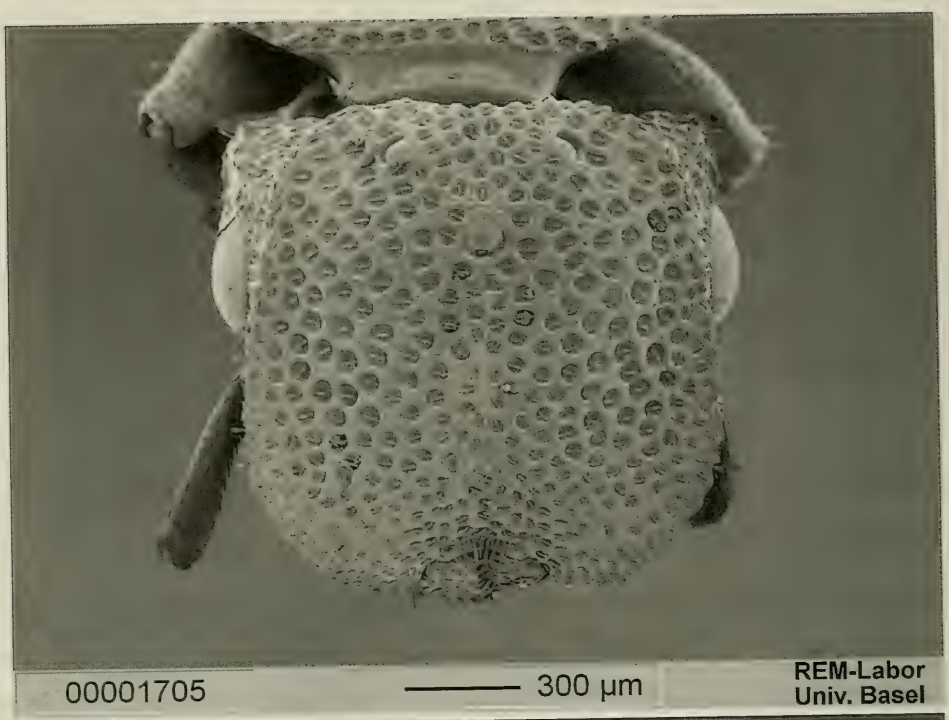


Fig. 203. *Cephalotes persimilis* DE ANDRADE. Gyne from San Bernardino, Paraguay: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 6.60–8.40; HL 1.16–1.56; HW 1.20–1.64; EL 0.32–0.37; PW 1.08–1.56; PeW 0.55–0.75; PpW 0.70–0.90; HBaL 0.40–0.50; HBaW 0.15–0.18; CI 101.3–105.9; PI 104.2–111.1; PPeI 196.4–226.7; PPpI 154.3–188.9; HBaI 34.1–40.0.

Male. - Head (eyes included and mandibles excluded) 1/2 broader than long. Vertexal angles gently convex in dorsal view. Frontal carinae marginate or not, not surpassing the first ocellus and diverging posteriorly. Frons flat. Clypeus posteriorly convex and almost straight anteriorly. Mandibles strongly carinate. Scapes thick, twice longer than the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotal sides slightly diverging and carinate. Mesonotum and scutellum almost flat in side view; median Mayrian furrow superficially impressed. Propodeum slightly lower than the rest of the mesosoma, with differentiate basal and declivous faces; basal face and anterior part of the declivous face convex; propodeal sides each with a thin lateral carina converging posteriorly.

Pedicel convex and very broad. Petiole slightly narrower than the postpetiole and with concave anterior face; petiole and postpetiole arched laterally.

First gastral tergite almost twice as broad as the maximum postpetiolar width.

Legs with femora relatively inflated.

Genitalia and subgenital plate as in Fig. 204.

Sculpture. Head punctate, irregularly foveolate on the posterior fourth, with oblique rugosities on the vertexal angles, longitudinal between the ocelli until the frontal carinae, transversal in front of the eyes and between the scapes. Ventral part of the head punctate, irregularly foveolate-rugulose, the rugae oblique around the eyes and irregularly longitudinal on the middle. Pronotum, mesonotum and scutellum superficially and minutely reticulate, subopaque, sparsely and superficially foveolate and longitudinally rugose, the rugae generally thin, more impressed on the Mayrian furrows and on the scutellum. Propodeum minutely reticulate, shining or not, with thick longitudinal rugosities prolonging backwards. Pedicel minutely reticulate-punctate, superficially shining and completely covered by longitudinal rugosities. Pleurae moderately shining and longitudinally rugose, the rugae less impressed on the metapleurae and on one specimen on the lower part of the mesopleurae as well. Gaster and legs almost completely shining.

Pilosity. Body with long, flexuous hairs, sparser on the gaster and on the legs. Gaster and legs with additional hairs subdecumbent to decumbent, shorter than the flexuous ones. Funiculi densely covered by thin, short, decumbent hairs; similar hairs but thinner, sparser and slightly longer on the legs and on the gaster.

Colour. Black. Pedicel, gaster and legs brown.

Measurements (in mm) and indices: TL 6.00–6.84; HL 0.80–0.84; HW 1.04–1.08; EL 0.42–0.43; PW 1.00–1.20; PeW 0.65–0.71; PpW 0.72–0.77; HBaL 0.50–0.53; HBaW 0.11–0.13; CI 128.6–130.0; PI 90.0–104.0; PPeI 153.8–169.0; PPpI 138.9–155.8; HBaI 22.0–24.5.

Material examined. - **Brazil:** no further locality, 1 gyne [MNHN]. Piauí: Canto do Buriti, 18–22.XI.1991, 2 workers, C. R. F. Brandão [MZSP]; Floriano, 05–12.XI.1991, 1 worker, Amarante et al. [MZSP]; 5 km E Oeiras, Fazenda Talhada, 13–17.XI.1991, 1 worker, C. R. F. Brandão & P. Moutinho [MZSP]. Ceará: no further locality, 5 workers (partly labelled as *maculatus* var. *cearensis* type and mixed with true *maculatus*), Rocha [MHNG]. Pará: no further locality, XII.1894, 1 worker (syntype of var. *nevadensis*), Göldi [MHNG]. Goiás: Alvorada do Norte, Fazenda Mattos, 1 worker, 08–12.VII.1991, C. R. F. Brandão [MZSP]. Bahia: Tanquinho, Feira de Santana, 08.XII.1953, 1 worker (paratype), 2 soldiers (holotype and paratype), C. R. Gonçalves [MZSP]; Itaberaba, Fazenda Riacho do Uruçu, 01–05.XII.1990, 3 workers, C. R. F. Brandão, J. M. Diniz & P. S. Oliveira [MZSP]. Distrito Federal: Reserva Biológica Águas Emendadas, 27–30.VI.1991, 25 workers, 7 soldiers, C. R. F. Brandão, M. L. Françoso & A. A. Reis [MZSP]. Mato Grosso: no further locality, 1 worker, 1 gyne, Germain [MCSN]; Utiariti, Rio Papagaio, VIII.1962, 1 gyne, K. Lenko [MZSP]. Mato Grosso do Sul: Corumbá, Fazenda Santa Blanca, 8.XII.1960, 1 worker, K. Lenko [MZSP]; Imbirussú-Corumbá, 1.XII.1960, 23 workers, K. Lenko [MZSP]. Minas Gerais: Pirapora, 15 workers, 4 soldiers, 2 gynes, 1 male, E. Garbe

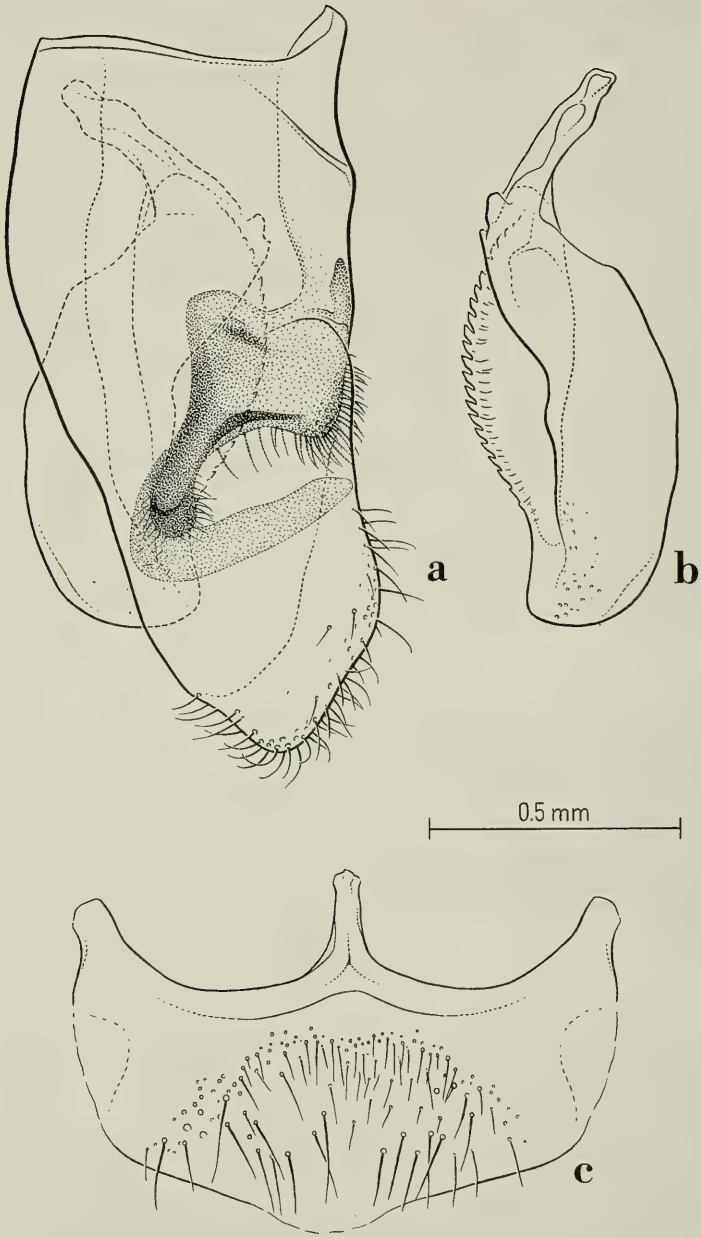


Fig. 204. *Cephalotes persimilis* DE ANDRADE. Male from Pirapora (Minas Gerais), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

[NHMB]; Januaria, 1 worker, GONÇALVES [MZSP]; Piraporinha, 22.XI.1948, 1 gyne, GONÇALVES [MZSP]. São Paulo: Onda Verde, Fazenda São João, I.1946, 1 gyne, F. LANE [MZSP]; Agudos, 28.I.1954, 1 worker, C. GILBERT [MZSP]; Pirapora, VI.1912, 6 workers, 3 soldiers, GARBE [MCZC, MZSP].

Argentina: Formosa: Laishi, 1 worker, ZURFLÜH [NHMB]; Mision Laishi, XII.1948, 1 male, GOLBACH [NHMB].

Paraguay: no further locality, 6 workers, BOHLS [MCSN]. Asunción: San Bernardino, in Stengel, 23 workers, 2 soldiers and 1 gyne, FIEBRIG [MHNG, NHMB].

Discussion. - *C. persimilis* has been previously confused with *grandinosus*. It can be distinguished from the true *grandinosus*, in the worker, soldier and gyne by the smaller and more regular foveae on the cephalic dorsum (see e. g. Figs. 198 and 205). The sister species of *persimilis* is *persimplex*, also previously confused with *grandinosus*. The main characters distinguishing these two species are given under *persimplex*.

Some of the workers listed in the material examined (all those from Distrito Federal, Goiás, Ceará, one from Itaberaba, some from Pirapora, Minas Gerais, and Pirapora, São Paulo) show the membranaceous expansions of the body flatter, the margin of the expansions of the propodeum crenulate and beset by minute hairs; otherwise, these specimens agree in all other characters with *persimilis*. The series from Pirapora, MG, in the SANTSCHI collection and the one from Pirapora, SP, in the KEMPF collection (both collected by GARBE) might be erroneously labelled, i.e. they can come from only one locality. Since a city named Pirapora exists in both states we prefer to leave the localities as they are given in the original labels. Both these series comprise a mixture of workers with the previously mentioned morphology and workers with the normal *persimilis* habitus. The male of *persimilis* is almost of the same size of the gyne, a condition unique among all other known *Cephalotes* males so far and approaching the condition *Procryptocerus* where the males are regularly slightly larger than the gynes. The *persimilis* males exhibit another remarkable character: the inflated femora as they are known for males of the members of the *laminatus* and *pusillus* clades and for *Procryptocerus*.

Distribution: Brazil, Argentina and Paraguay.

Cephalotes persimplex DE ANDRADE new species
Figs. 205, 206, 207, 208

Paracryptocerus grandinosus (SMITH), KEMPF, 1952: 12, fig. 13. Gyne (nec worker and soldier). Nec SMITH, 1860. Misidentification.

Type material: Holotype worker, Reyes, Bolivia, Oct. 1921–22, Mulford Biol. Exp., W. M. MANN [USNM]; paratypes 8 workers, 3 soldiers, 1 gyne (USNM), 1 worker, 1 soldier and 1 gyne, all same data as the holotype (MZSP).

Derivatio nominis: from the Latin *persimplex* = very easy (Tacitus), referred to the facility with which this species can be separated from *C. grandinosus* with which it had been confused.

Diagnosis. - A member of the *grandinosus* clade characterised in the worker and soldier by the body with thick, whitish hairs, and, in the gyne, by the frontal carinae almost without crenulation and hairs.

Worker (Fig. 205). - Head subquadrate; frons convex in the middle. Frontal carinae covering large part of the mandibles, slightly upturned above the eyes. Vertexal angles membranaceous, obtuse, converging and narrowing before the middle of the vertexal border. Mandibles with thick, with a lateral carina visible in side view.

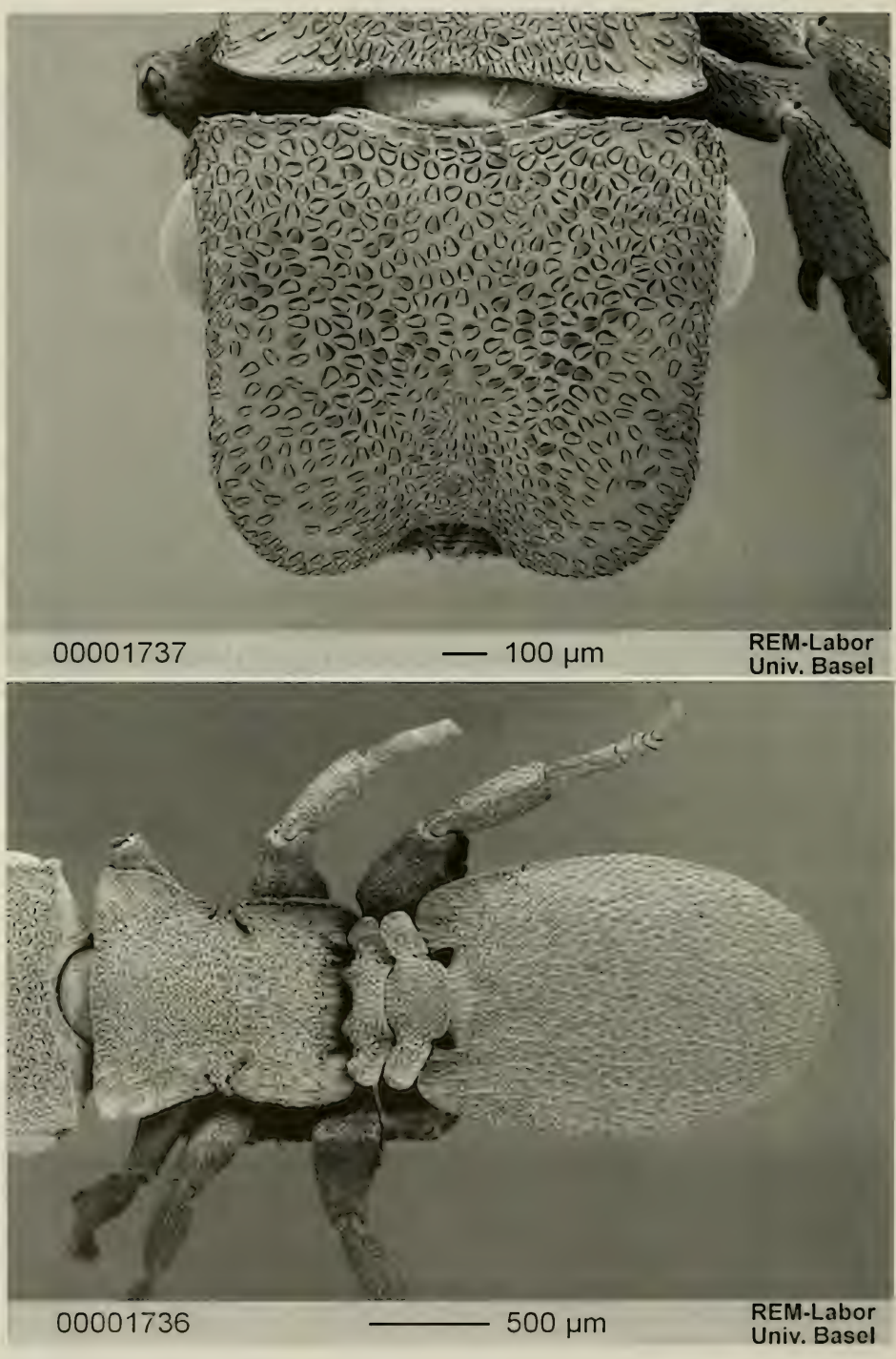


Fig. 205. *Cephalotes persimplex* DE ANDRADE. Worker from Reyes, Bolivia: head (top) and meso- and metasoma (bottom) in dorsal view.

Mesosoma gently convex. Scapular angles absent or not visible in dorsal view. Anterior pronotal border straight; pronotal sides with a broad membranaceous expansion, anteriorly obtuse to truncate and narrowing posteriorly. Promesonotal suture absent. Mesonotum with a pair of long, triangular, membranaceous teeth wider than the pronotal lamellae posteriorly. Propodeal suture impressed. Declivous face of the propodeum gently sloping backwards. Basal and declivous propodeal faces with a broad membranaceous expansion, the border starting on the beginning of the basal face and strongly projected anteriorly, almost reaching the mesonotal spines and broadening backwards.

Petiole with concave anterior face laterally marked by a pair of round denticles; petiolar dorsum sloping anteriorly. Sides of the petiole with a broad, wing-shaped, membranaceous expansion with round tip. Postpetiole slightly convex dorsally; postpetiolar sides with another broad, wing-shaped, membranaceous border with round tip.

Gaster oval. First gastral tergite anterolaterally with a broad, membranaecous border reaching the stigma.

Mid and hind femora angulate; hind femora with two membranaceous crests on the two distal thirds, one on the dorsal face and another on the ventral face; mid femora with a short dorsal carina or a narrow membranaceous crest and ventrally with a crest as high as the one on the hind femora but shorter. Mid and hind basitarsi with flat and broad base.

Sculpture. Head dorsum, mesosoma and peduncular segments superficially punctate, with dense, small, foveae broader than their interspaces, sparser on the frontal carinae and smaller on the border of the head dorsum, and on the pedicel. Ventral face of the head with the same type of sculpture as on the dorsum but the foveae less dense and the punctures more impressed. Concavity of the declivous face of the propodeum with faint, longitudinal rugosities. Gaster and legs punctate and densely covered by superficial, small foveae; the punctures less impressed on the posterior half of the first gastral sternite. Anterior third of the first gastral segment with thin, longitudinal rugosities. Pleurae reticulate and with superficial foveae and thin, longitudinal, rugosities. Membranaceous border of mesosoma, pedicel and gaster punctate and with thin, longitudinal rugosities.

Pilosity. Each fovea with an appressed, broad hair; similar hairs but not originating from the foveae on the membranaceous borders of the body. Frontal carinae over the eyes and posterior part of the gastral sternites with sparse, clubbed hairs. The sternites bear, in addition a few long, thin, slightly pointed hairs.

Colour. Body light brown with whitish appearance due to the white pilosity. Frontal carinae opaque yellow. Membranaceous borders of the body equally whitish and semi-transparent. Tarsi brown.

Measurements (in mm) and indices: TL 3.80–4.88 HL 0.88–1.08; HW 1.04–1.28; EL 0.27–0.32; PW 0.96–1.24; PeW 0.56–0.76; PpW 0.56–0.80; HBaL 0.27–0.35; HBaW 0.12–0.14; CI 118.2–118.5; PI 103.2–108.3; PPeI 163.1–171.4; PPpI 155.0–171.4; HBaI 40.0–44.4.

S o l d i e r (Fig. 206). - Head disc subquadrate, with raised and differentiate border; sides of the disc not covering completely the eyes and broadening anteriorly. Floor of the disc concave with a short tumulus in the middle. Vertexal angles obtuse, completely separate from the disc and with well marked border. Mandibles laterally carinate and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border straight. Humeral angles with a broad, obtuse, membranaceous border with straight sides posteriorly up to the middle of the pronotal sides where it continues into the pronotal carina. Posterior half of the pronotal sides strongly converging. Pronotal carina developed, each half posteriorly convex and diminishing in height towards the middle of the pronotum. Pronotal suture, on the dorsum, impressed on the sides only. Promesonotal suture deeply impressed. Mesonotal sides with a pair of broad, triangular teeth followed by a pair of thin, pointed, membranaceous denticles. Propodeum with differentiate basal and declivous faces; sides of the basal face with a membranaceous border, the border forming anteriorly a pair of obtuse teeth directed anteriorly, followed by a short notch and by a convexity converging posteriorly into a pair of small denticles. Declivous face of the propodeum narrowing posteriorly and with a membranaceous border.

Petiole with concave anterior face; wing-shaped membranaceous expansions with rounded tips arise laterally on the two anterior thirds of the petiole. Postpetiole gently convex dorsally, with similar wing-like lateral expansions as the petiole but directed anteriorly.

Gaster oval. First gastral tergite anterolaterally with a pair of broad membranaceous borders not reaching the stigma posteriorly.

Legs. As in the worker.

Sculpture. As in the worker except for the punctures, more impressed on the whole body, for the integumental foveae sparser on the head dorsum and for the anterior third of the first gastral tergite with smaller foveae.

Pilosity. As in the worker but with the anterior fourth of the first gastral tergite with hairs as broad as the one originating from each foveae, and the vertexal angles with rare hairs as the clubbed ones over the eyes.

Colour. As in the worker.

Measurements (in mm) and indices: TL 5.32–5.38; HL 1.16–1.22; HW 1.36–1.44; EL 0.30–0.32; PW 1.40–1.48; PeW 0.70–0.76; PpW 0.68–0.72; HBaL 0.31; HBaW 0.14–0.15; CI 117.2–118.0; PI 97.1–97.3; PPeI 211.4–225.8; PPpI 205.5–205.9; HBaI 45.2–48.4.

G y n e (Fig. 207). - Head disc present. Head dorsum slightly concave on its anterior half and gently convex posteriorly. Frontal carinae weakly crenulate, expanded anteriorly, converging posteriorly and connected by a slightly convex carina on the vertex. Vertex with a superficial depression between the pair ocelli. Vertexal angles broad, obtuse and marginate. Eyes visible in full dorsal view. Ocelli remote from the posterior border of the head disc. Anterior clypeal border concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of round, broad, membranaceous teeth converging posteriorly and connected with a faint pronotal carina often shortly interrupted in the middle. Pronotal sides posterior to the angles straight. Promesonotal suture impressed. Lower mesopleurae with a denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face strongly convex and ending in a stout, round tooth posteriorly; declivous face converging posteriorly and with a narrow membranaceous border.

Anterior face of the petiole concave; petiolar dorsum gently sloping anteriorly; petiolar sides with a narrow, convex membranaceous border. Postpetiole convex; anterior half of its sides with a pair of round teeth directed anteriorly.

Gaster with a pair of lobes protruding anteriorly.

Wings as in Fig. 208.

Legs. Fore coxae angulate anteriorly. Hind femora gently curved dorsally and superficially carinate on the distal part of the dorsum; posterior margin of the ventral face of the mid and hind femora with a narrow, membranaceous crest. Mid and hind basitarsi flat, with broad base.

Sculpture. Head dorsum superficially punctate, with dense, small, deep, round foveae diminishing in size anteriorly. Frontal carinae punctate and with rare, superficial foveae. Ventral part of the head and propleurae with superficial, irregular foveae, the foveae denser on the ventral sides of the head. Pronotum punctate with much denser foveae on the sides than on the middle. Mesonotum and scutellum with similar foveae as on the head dorsum but sparser and diminishing in size on the posterior half of the scutellum. Basal face of the propodeum, pedicel and upper mesopleurae densely covered by deep, small foveae. Declivous face of the propodeum and lower meso- and metapleurae punctate and with thin, longitudinal rugosities. First gastral segments densely reticulate; their anterior third with thin, irregular, longitudinal rugosities and with piligerous foveae larger and denser than on its remaining surface; the reticulation less impressed on the posterior half of the first gastral sternite. Legs reticulate and with sparse piligerous foveae.

Pilosity. Each fovea with an appressed, broad hair. Frontal carinae over the eyes, vertexal angles, mesosoma, pedicel, first gastral tergite and legs with rare, suberect, clubbed hairs; similar hairs but longer on the apex of the gaster. Sternites, distally, with long, sparse, thin, slightly pointed hairs.

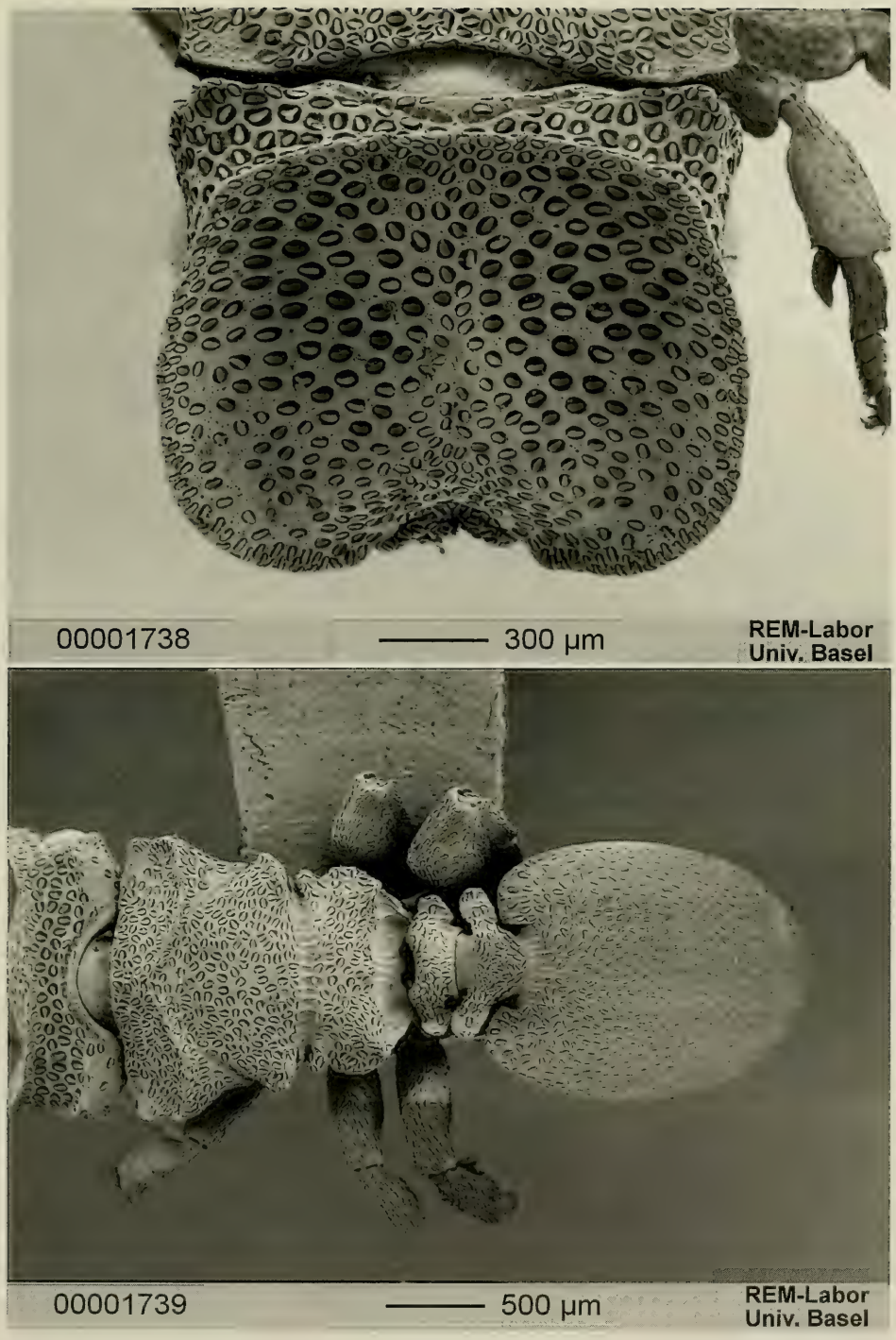


Fig. 206. *Cephalotes persimplex* DE ANDRADE. Soldier from Reyes, Bolivia: head (top) and meso- and metasoma (bottom) in dorsal view.

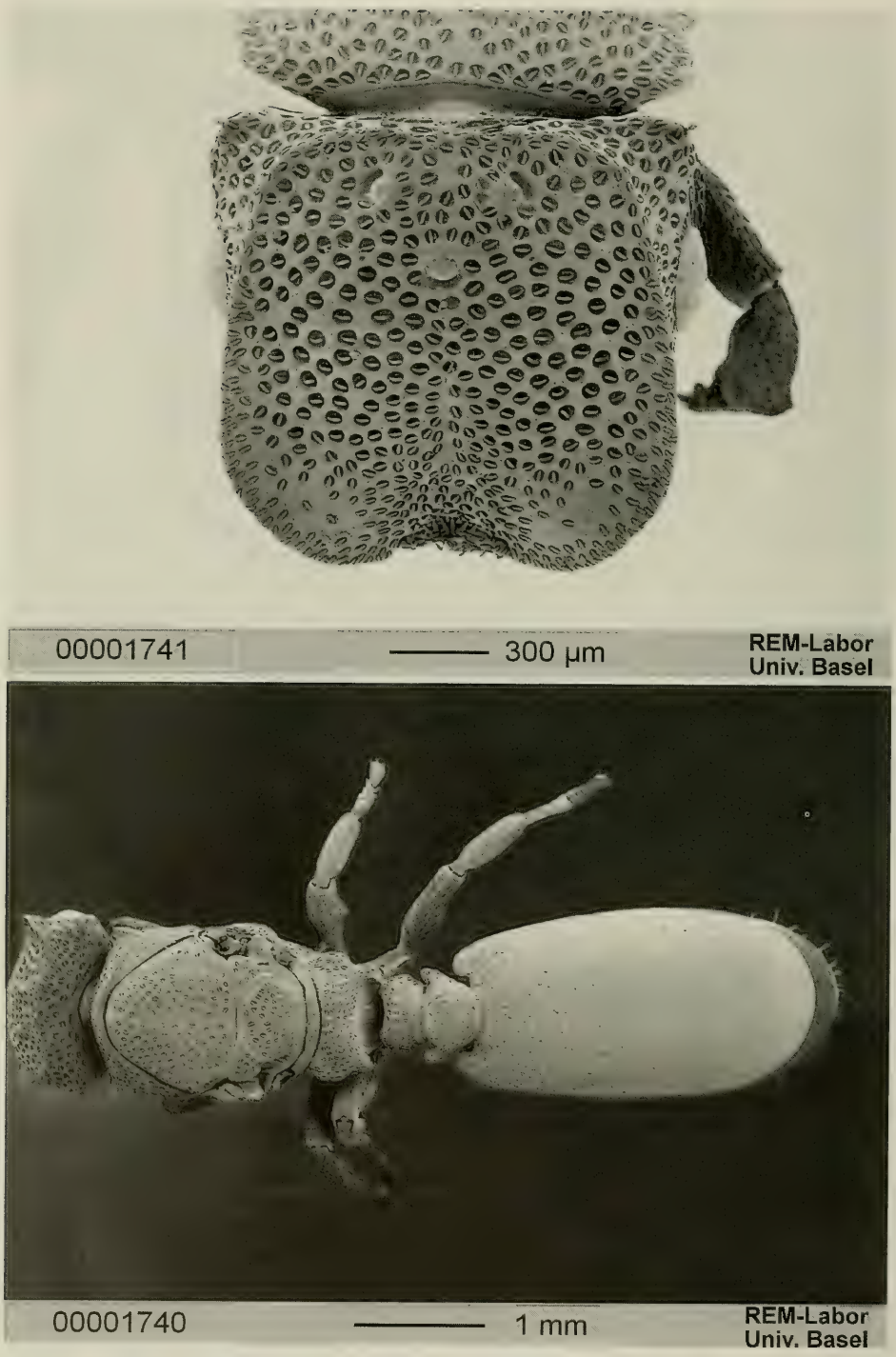


Fig. 207. *Cephalotes persimplex* DE ANDRADE. Gyne from Reyes, Bolivia: head (top) and meso- and metasoma (bottom) in dorsal view.

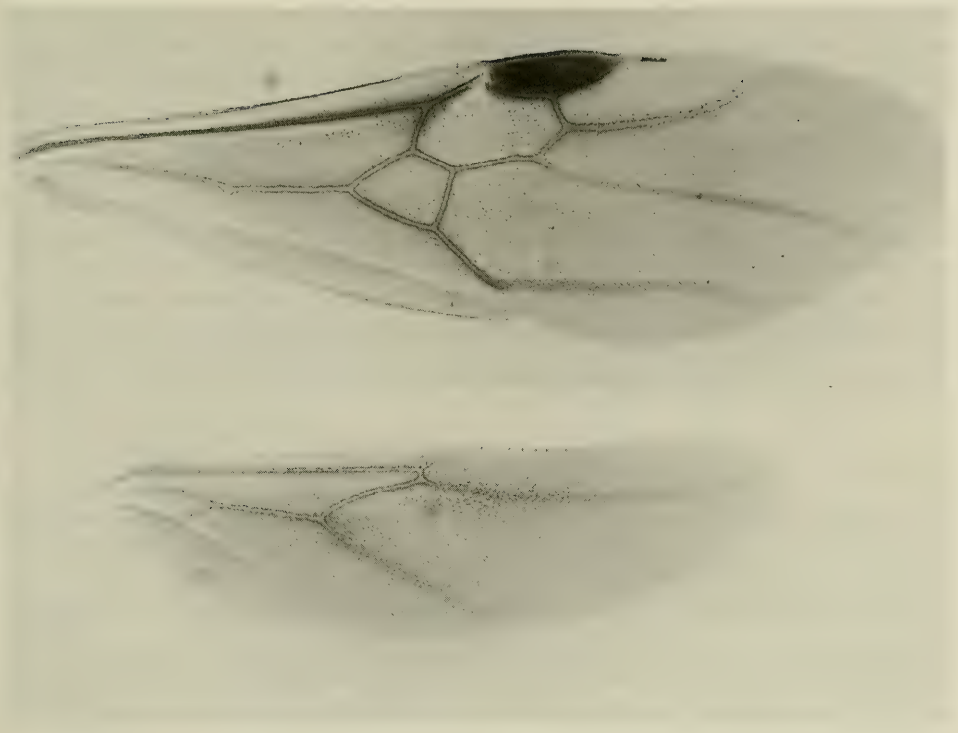


Fig. 208. *Cephalotes persimplex* DE ANDRADE. Gyne from Reyes, Bolivia, fore and hind wings.

Colour. Light brown. Frontal carinae yellowish-opaque and semitransparent. Tarsi brown. First gastral tergite with a pair of dark brown maculae on the middle of the dorsum faintly connected medially.

Measurements (in mm) and indices: TL 7.26–8.12; HL 1.32–1.40; HW 1.40; EL 0.34–0.37; PW 1.30–1.36; PeW 0.56–0.64; PpW 0.74–0.84; HBaL 0.44; HBaW 0.16; CI 100.0–106.1; PI 102.9–107.7; PPeI 212.5–232.1; PPpI 161.9–175.7; HBaI 36.4.

Material examined. - **Brazil**: Acre: Cruzeiro do Sul, 11.III.1983, 4 workers, F. H. CAETANO [MZSP]; same locality, 07.VI–14.VII.1983, 1 worker, R. H. PIRES [MZSP]. Mato Grosso: no further locality, 1886, 2 workers, GERMAIN [MCSN]; Limoeiro, 10 km S of Ilha de Taiamã, 08.VIII.1980, 2 workers, C. R. F. BRANDÃO [MZSP]; Ilha de Taiamã, R. Paraguai, 10.VIII.1980, 1 worker, C. R. F. BRANDÃO [MZSP]. Minas Gerais: Cachoeira Marimbondo, 04.III.1965, 2 workers, VIZOTTO [MZSP].

Bolivia: Beni: Reyes, X.1921–22, 9 workers, 4 soldiers, 2 gynes (type series), Mulford Biol. Exp., W. M. MANN [USNM, MZSP]; Rurrenabaque, X.1921–22, 2 workers, Mulford Biol. Exp., W. M. MANN [MCZC]. La Paz: Ixiamas, XII.1921–22, 1 worker, Mulford, Biol. Exp., W. M. MANN [USNM].

Discussion. - *C. persimplex* is, together with *persimilis*, one of the two species formerly confused with *grandinosus*. It can be easily distinguished from the true *grandinosus* by the smaller foveae on the cephalic dorsum and by the broad whitish body hairs. Its sister species is *persimilis*, also distinct from *grandinosus* in

the present study. Both species share in the workers the vertexal angles obtuse and narrowly membranaceous, the frontal carinae little crenulate and weakly upturned over the eyes, and, in the soldiers and gynes, the foveae on the cephalic disc regular. *C. persimplex* is superficially similar to *persimilis* but the workers of *persimilis* can be recognised from those of *persimplex* by the curved and thinner body hairs and by the mesosoma with irregular foveae superimposed by longitudinal rugosities (see Figs. 201 and 205). The soldiers of *persimplex* differ from those of *persimilis* by the floor of the disc more concave and with raised border, by the thicker and denser appressed hairs and by the superficially crenulate border of the disc (see Figs. 202 and 206); the gynes of *persimplex* differ from those of *persimilis* by the thicker hairs, by the less convex head dorsum and by the weakly crenulate frontal carinae (see Figs. 203 and 207).

Distribution: Brazil and Bolivia.

5.6.13. The *pallens* clade

A relatively large clade containing ten Recent species. It roughly corresponds to the former subgenus *Cyathomyrmex* but *setulifer*, formerly included in *Cyathomyrmex*, has been excluded from it.

The members of this clade are characterised by the three following synapomorphies:

1. Frontal carinae of the workers broadly incised over the eyes.
2. Frontal carinae concolour with the rest of the head.
3. Soldier and gyne with the disc covering the mandibles.

An additional probable synapomorphy for the species of this clade is a character not considered in our data matrix: the capacity of the soldiers to secrete camouflage material. We have evidence of soldiers with the head more or less covered by such material for all the species of the clade. We did not include the secretion of camouflage material in our list of characters because of the difficulty to obtain evidence of its absence for a number of species. This trait, however, is homoplastically present also outside the *pallens* clade at least in *setulifer*, *coffeae*, and, probably, *patei*.

These three species, however, cannot be considered members of the *pallens* clade since they lack at least two important sets of synapomorphies, i. e. most of those already listed above as characterising the *pallens* clade (*setulifer* soldiers and gynes, represent the sole exception since they have a disc covering the mandibles) and the following important synapomorphies of a broader basalmost clade including our *pallens*, *grandinosus* and *pinelii* clades: antennal club two-jointed, secondary loss or great reduction of the scapular angles in dorsal view, and median depression of the disc. Forcing either of these species to belong to the *pallens* clade would cost respectively 9 additional evolutionary steps for *setulifer*, 8 for *coffeae* and 7 for *patei*. Forcing all three species together to join the *pallens* clade would cost a minimum of 16 additional evolutionary steps. These results have been obtained after only one heuristic search for each hypothesis and with a different constraint per search.

The species we recognise as belonging to the *pallens* clade represent a very homogeneous set and are often difficult to distinguish from each other, particularly in the worker caste. This situation is worsened by the fact that these ants appear to exhibit the greatest variability within *Cephalotes* in sculpturation and in body size. In this sense, one of the oldest available names for a species of this clade, SMITH's (1876)

varians, was premonitory. KEMPF (1958 a) already tried to split the species and subspecies described in *Cyathomyrmex*. His efforts have been unsuccessful because of the limited number of soldiers associated with workers available to him.

Species included in the clade: *decolor*, *decoloratus*, *jamaicensis*, *pallens*, *pallidoides*, *pallidus*, *patellaris*, *pellans*, *porrasi*, *varians*.

Cephalotes varians (F. SMITH) new combination
Figs. 209, 210, 211, 212, 213, 384 C

Cryptocerus varians F. SMITH, 1876: 606, pl. 11, fig. 4. Worker. Original description. Type locality: Cuba. Type material 4 syntype workers on the same pin labelled „from Cuba, varians, Sm. Type (Cuba)" in BMNH, examined.

Cryptocerus varians SMITH, WHEELER, 1905: 102, pl. 7, figs. 1–6. Worker, soldier, gyne, male.

Cryptocerus varians WHEELER, 1910: fig. 53. Worker, soldier, gyne, male.

Cyathocephalus varians, FOREL, 1923: fig. 30. Soldier, gyne, male. First combination in *Cyathocephalus*.

Paracryptocerus varians (F. SMITH), M. R. SMITH, 1951: 825. First combination in *Paracryptocerus*.

Paracryptocerus varians (F. SMITH), WHEELER & WHEELER, 1954 b: 156. Larva.

Paracryptocerus varians (F. SMITH), KEMPF, 1958 a: 155, pl. 8, figs. 7, 8. Worker, soldier. Partim.

Zacryptocerus varians (KLUG), WILSON, 1976 b: 354. First combination in *Zacryptocerus*.

Zacryptocerus varians, WHEELER & HÖLLDOBLER, 1985: figs. 1–3. Soldier.

D i a g n o s i s . - A member of the *pallens* clade characterised by the following apomorphies: in the worker propodeal sides unarmed or with a narrow membranaceous margin medially denticulate, in the soldier and in the gyne by the combination of head disc with foveae contiguous each other, in the soldier by the outer face of the hind femora superficially carinate, by the head longer than broad, and, in the gyne, by the petiole and postpetiole without or with reduced lateral expansions.

W o r k e r (Fig. 209). - Head slightly broader than long. Frons gently convex. Frontal carinae deeply incavate over the eyes and converging anteriorly. Vertexal angles with a pair of narrow, round or obtuse membranaceous expansions. Membranaceous expansions of the vertexal angles converging and not connected medially. Vertexal margin with a short „neck". Funicular club with two joints. Mandibles with superficial lateral carina.

Mesosoma. Scapular angles not visible in dorsal view. Anterior pronotal border convex. Pronotal sides with a pair of narrow, membranaceous expansions gently converging posteriorly. Promesonotal suture, in dorsal view, superficially impressed in some specimens only. Mesonotal sides with a pair of teeth truncate or pointed. Propodeum with poorly differentiate basal and declivous faces. Propodeal sides medially with a pair of triangular, membranaceous teeth of variable size; some specimens with the propodeal sides simply marginate or with a pair of narrow membranaceous expansions including the median teeth.

Petiole. Anterior face slightly concave. Petiolar sides with a pair of short, truncate or pointed teeth. Postpetiolar node convex dorsally; postpetiolar sides with a pair of spines, pointed or round and directed forwards.

Gaster. Oval and with a pair of anterolateral membranaceous expansions variably developed and not surpassing the stigma posteriorly.

Hind and mid femora gently angulate; their distal part with a dorsal longitudinal carina; the carina less impressed on the mid femora. Mid and hind basitarsi flat, with the proximal part broader than the distal one.

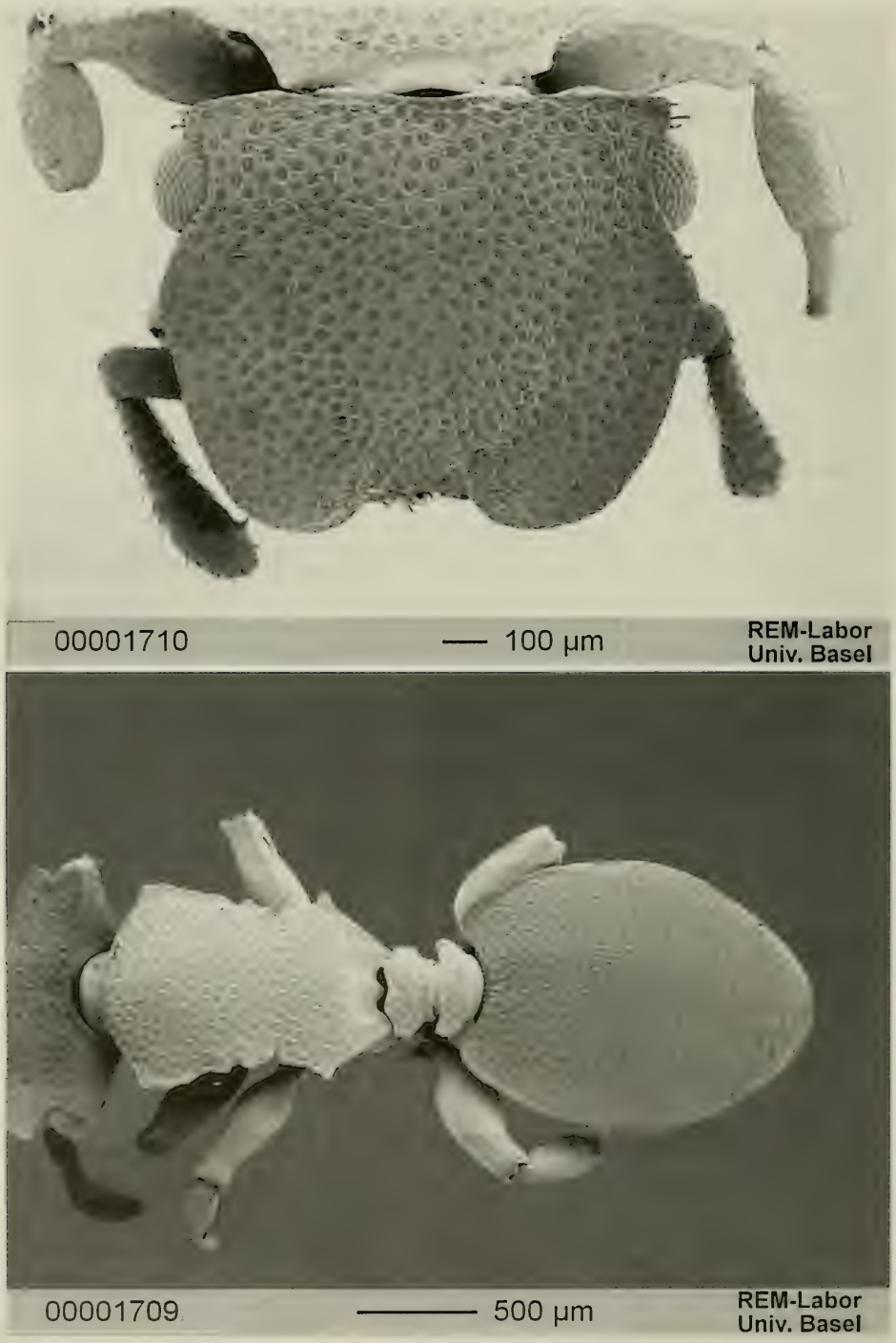


Fig. 209. *Cephalotes varians* (SMITH). Worker from Andros Island, Bahamas: head (top) and meso- and metasoma (bottom) in dorsal view.

Sculpture. Head dorsum and mesosoma minutely reticulate and with superimposed superficial, dense foveae, shallower on the frontal carinae, sparser on the frons and denser on the mesosoma; some specimens with dense foveae on the whole head dorsum. Ventral part of the head reticulate and superimposed to foveae as on the frontal carinae on its anterior half. Pedicel minutely reticulate and with small, superficial foveae. Pleurae reticulate. First gastral tergite reticulate and with sparser, very superficial foveae, larger and more impressed on the anterior third. Gastral sternites and legs reticulate and with minute, superficial foveae, more impressed and denser on the outer face of the tibiae. Center of the first gastral sternite shining.

Pilosity. Each fovea with an appressed hair. Posterior half of the frontal carinae, vertexal angles, first gastral tergite and sternite, posterior border of the remaining gastral segments, and legs with rare clubbed hairs, slightly thinner on the first gastral sternite. Parts of the gaster and of the legs without foveae with short, appressed, very thin hairs. Gastral sternites with additional, rare, long, pointed hairs.

Colour. Ferruginous to brown with the frontal carinae and the membranaceous expansions of the body slightly lighter.

Measurements (in mm) and indices: TL 3.36–4.97; HL 0.82–1.16; HW 0.88–1.28; EL 0.19–0.26; PW 0.70–1.06; PeW 0.46–0.68; PpW 0.45–0.60; HBaL 0.27–0.36; HBaW 0.10–0.13; CI 107.3–118.5; PI 116.0–125.7; PPeI 138.2–216.7; PPpI 155.5–196.2; HBaI 34.3–38.7.

S o l d i e r (Fig. 384 C). - Head disc suboval and covering completely the mandibles in dorsal view. Border of the disc strongly raised and with minutely crenulate margin, the crenulation more impressed on the posterior half. Floor of the disc medially with a small tumulus. Posterior part of the disc medially depressed. Vertexal angles completely separate from the disc, obtuse and with crenulate margin. Eyes slightly convex and hidden by the disc. Mandibles laterally carinate.

Mesosoma. Humeral angles with a pair of obtuse or slightly pointed teeth or with narrow membranaceous expansions. Pronotal sides gently converging posteriorly. Pronotal carina well marked, with crenulate margin and interrupted medially. Pronotal suture in dorsal view more impressed on the sides. Promesonotal suture deeply impressed. Mesonotal sides with a pair of broad, triangular teeth with almost round tip; some specimens with an additional pair of minute denticles. Propodeum with differentiate basal and declivous faces; sides of the basal face with two pairs of small, round swellings followed by a pair of stout teeth curved up and forwards in large specimens. Declivous face of the propodeum narrowing posteriorly.

Pedicel as in the worker but with narrower and shorter spines.

Hind femora dorsally gently angulate and with superficial carina in their distal part. Mid and hind basitarsi flat, with the proximal part broader than the distal one.

Gaster. Oval and with a pair of protruding lobes.

Sculpture. Head dorsum minutely punctate variably shining and with large, dense foveae, smaller on the tumulus and near the posterior border of the disc; foveae of the disc separated by thin interspaces. Sides of the head disc densely and irregularly foveolate, the foveae more superficial on the anterior half. Ventral part of the head punctate, variably shining; this sculpture covered by irregular, longitudinal rugosities on the posterior half and with small, dense, irregular foveae on the anterior half. Mesosoma minutely reticulate-punctate and with dense foveae, slightly irregular or oval on the pronotum, round on the mesonotum, small and superficial on the propodeum. Pedicel with similar sculpture as on the propodeum but with smaller foveae. Pleurae reticulate and with small, superficial foveae on the upper border. Gaster and legs with similar sculpture as in the worker but with slightly larger foveae.

Pilosity. Each fovea with an appressed or subdecumbent hair. Borders of the disc and sides of the head with many suberect, long, clavate hairs, sparser on the anterior border of the disc. Pronotum, first gastral segment, posterior border of the remaining gastral segments with rare, short clubbed hairs, denser on the first gastral sternite. Parts of the gaster and legs without foveae with short, appressed, thin hairs. Gastral sternites with additional rare, long, pointed hairs.

Colour. Dark ferruginous with slightly lighter gaster.

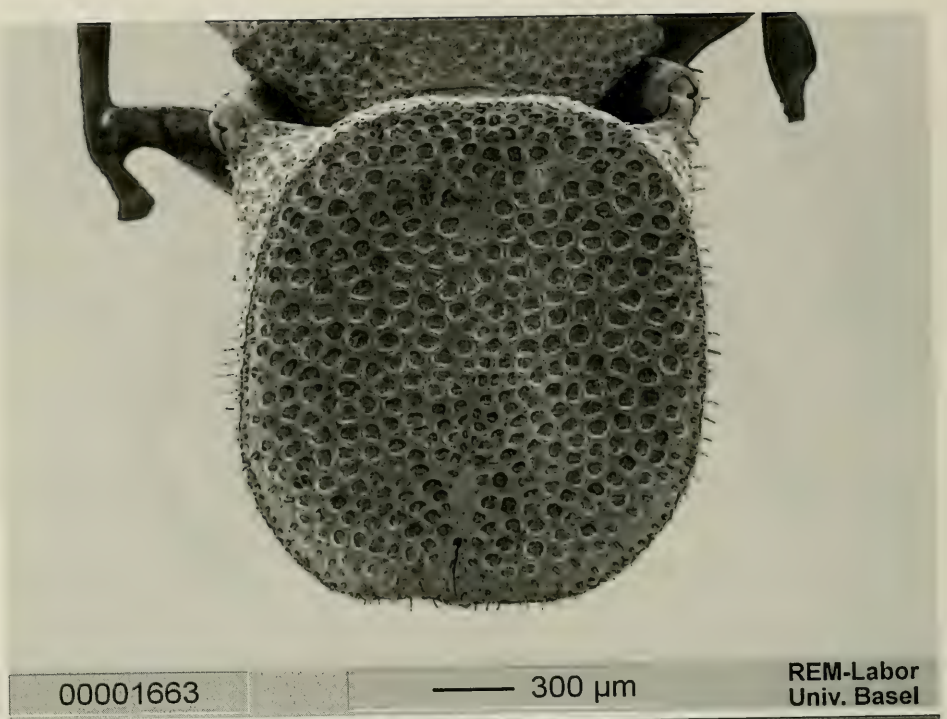


Fig. 210. *Cephalotes varians* (SMITH). Gyne from Plantation Key, Florida: head (top) and meso- and metasoma (bottom) in dorsal view.

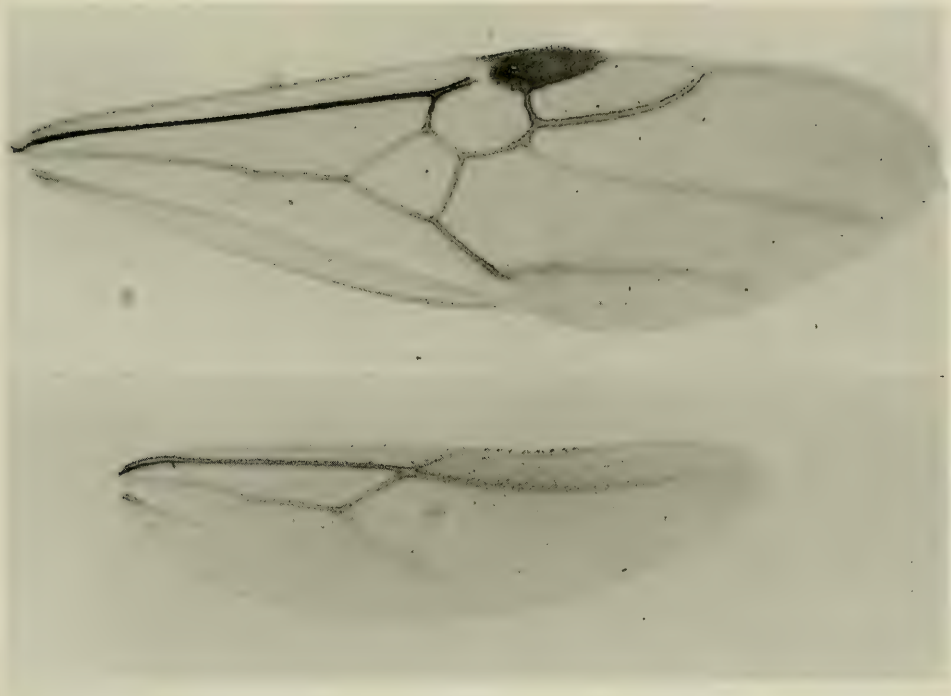


Fig. 211. *Cephalotes varians* (SMITH). Gyne from Plantation Key, Florida, fore and hind wings.

Measurements (in mm) and indices: TL 5.40–7.16; HL 1.44–1.96; HW 1.40–1.76; EL 0.30–0.33; PW 1.32–1.80; PeW 0.58–0.60; PpW 0.57–0.64; HBaL 0.32–0.39; HBaW 0.13–0.15; CI 84.8–97.2; PI 97.8–106.1; PPeI 227.6–305.1; PPpI 231.6–300.0; HBaI 37.1–40.6.

G y n e (Fig. 210). - Differing from the soldier as listed below.

Sides of the disc with lower borders and with the margin more crenulate. Posterior part of the disc with deeper median depression.

Mesosoma. Humeral angles with a pair of triangular teeth with pointed or obtuse tip. Pronotal carina lower. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly convex and posteriorly with a pair of teeth with round or pointed tip and slightly diverging backwards.

Wings as in Fig. 211.

Petiole. Anterior face oblique and concave. Petiolar sides unarmed. Postpetiole as in the soldier but with the lateral spines broader, shorter and truncate.

Gaster. Similar to the one of the soldier but much longer.

Legs with less impressed carinae on the outer face of the femora.

Sculpture. Head dorsum with deeper, larger and denser foveae. Foveae on the mesonotum sparser. Pleurae reticulate. Propleurae with thin, faint, rugosities sometimes oriented transversally or longitudinally. Border of the lower metapleurae with thin, longitudinal rugosities. Upper part and center of the lower mesopleurae with small foveae, deeper and denser on the upper mesopleurae.

Pilosity. As in the soldier except for the clubbed hairs which are more abundant on the mesosoma an on the gaster.

Colour. Dark ferruginous.

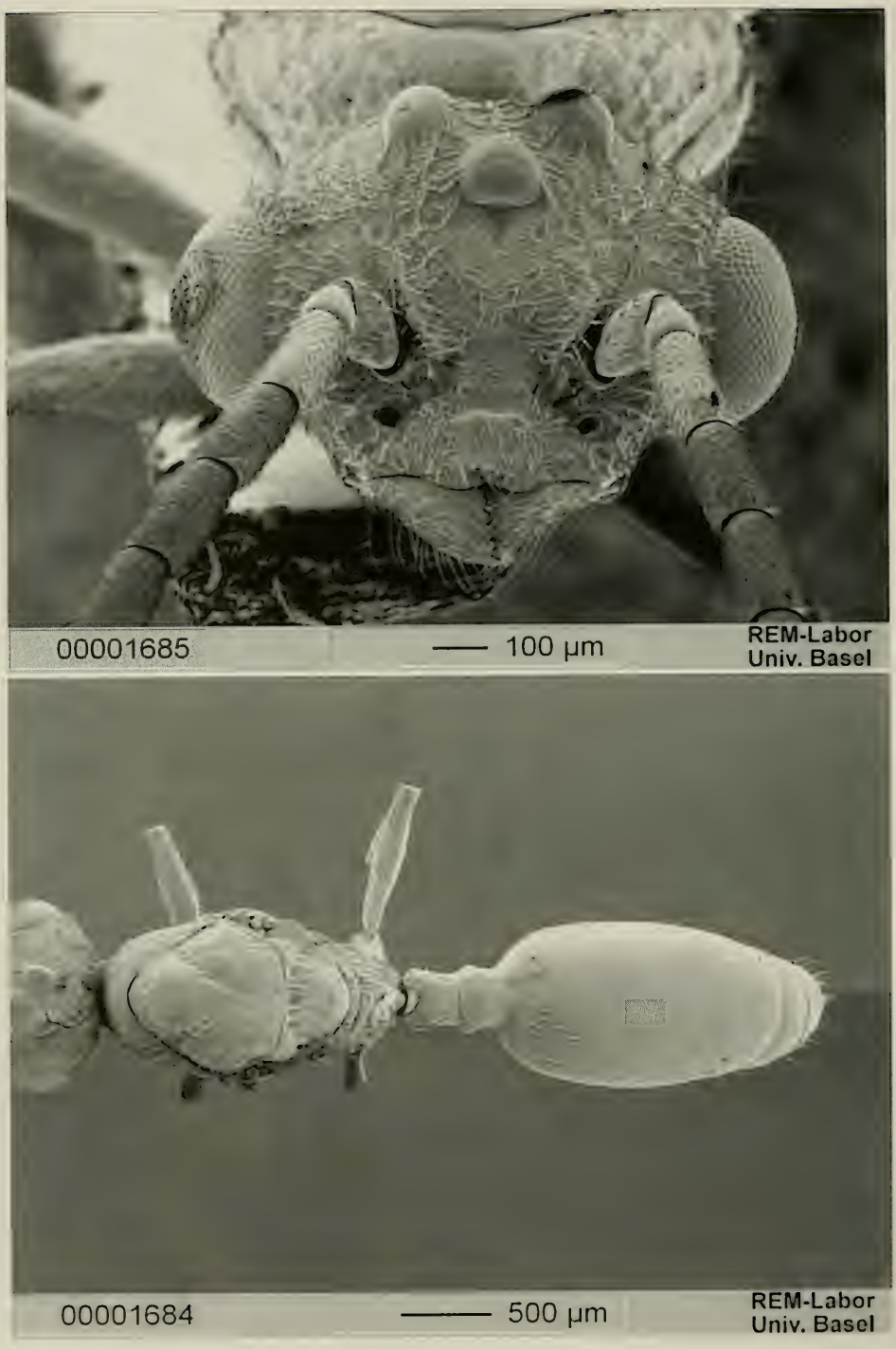


Fig. 212. *Cephalotes varians* (SMITH). Male from Cienfuegos, Cuba: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 7.52–8.36; HL 1.56–1.76; HW 1.44–1.58; EL 0.35–0.38; PW 1.32–1.56; PeW 0.51–0.56; PpW 0.57–0.64; HBaL 0.43–0.51; HBaW 0.15–0.17; CI 89.8–92.3; PI 101.3–109.1; PPeI 258.8–278.6; PPpI 231.6–243.7; HBaI 31.9–37.2.

M a l e (Fig. 212). - Head (eyes included) more than 1/3 broader than long. Vertexal angles converging to the vertexal margin. Vertex dorsally protruding, bearing salient ocelli. Compound eyes broadly convex, at mid head length. Frontal carinae very short and with a raised, convex border.

Frons flat and with a median, superficial sulcus. Clypeus convex posteriorly and incised anteriorly. Mandibles short and superficially carinate on the sides. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view with the sides diverging backwards. Mesonotum convex in side view; median Mayrian furrow variably impressed but always present. Scutellum convex, rounded posteriorly. Basal and declivous faces of the propodeum differentiate; basal face gently convex dorsally and slightly declivous; declivous face with converging sides.

Petiole with concave anterior face; posterior face gently convex and sloping posteriorly. Petiolar sides converging backwards, with a minute pair of denticles or unarmed. Postpetiole convex; its sides with a small, round median denticle.

Gaster as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 213.

Wings. As in the gyne.

Sculpture. Head dorsum reticulate and sparsely, irregularly rugose, some specimens only; this structure superimposed to few, superficial, foveae more regular and denser behind the pair ocelli. Ventral part of the head reticulate, irregularly rugose-foveolate. Pronotum, mesonotum and scutellum with superficial, minute reticulation and with foveae as on the posterior part of the head dorsum, the foveae shallower and sparser on the mesonotum and scutellum. Basal face of the propodeum reticulate and with generally irregular, longitudinal rugosities. Declivous face of the propodeum, pedicel and propleurae reticulate. Mesopleurae reticulate; center of the lower and upper mesopleurae superficially foveolate; lower mesopleurae with few additional, longitudinal rugosities. Metapleurae reticulate and with irregular rugosities on the upper part. Gaster superficially reticulate and subopaque to shining. Legs punctate with moderately shining femora.

Pilosity. Body with long, thin, flexuous, pointed, golden hairs, dense on the head, on the mesosoma and on the pedicel, sparser on the gaster and on the femora. Gaster and legs with similar hairs but shorter, appressed on the tergites, decumbent on the sternites and on the femora. Tibiae and tarsi with short, pointed hairs.

Colour. Dark ferruginous-brown with slightly lighter coxae, pedicel and gaster. Legs yellowish with darker tarsomeres.

Measurements (in mm) and indices: TL 4.39–5.20; HL 0.70–0.75; HW 0.84–0.92; EL 0.30–0.41; PW 0.75–0.84; PeW 0.33–0.40; PpW 0.35–0.45; HBaL 0.44–0.47; HBaW 0.07–0.08; CI 120.0–122.7; PI 109.5–112.0; PPeI 210.0–227.3; PPpI 186.7–214.3; HBaI 14.9–18.2.

M a t e r i a l e x a m i n e d . - **United States**: F l o r i d a : Miami, 23.VI.1945, 4 workers, 2 soldiers, Wm. Buren [MZSP]; Coconut Grove, 09.I.1991, 3 soldiers, 3 gynes, 2 males, W. M. Wheeler [MCZC]; Cards' Point, 8 workers, 2 soldiers, 8 males, Wheeler [MCZC]; Central Florida Keys, nr. Marathon, VIII.1974, 6 workers, E. O. Wilson [MCZC]; Key E-3, Rattlesnake Lumps, 08.X.1966, 8 workers, 1 soldier, E. O. Wilson & D. Simberloff [MCZC]; Key E–4 and E–5, East side of Ohio Key, Middle Keys, 17 & 28.VII.1966, 4 gynes, E. O. Wilson & D. Simberloff [MCZC]; Key E–7, Pt. Laura, nr. Jewfish Crk. 10.X.1966, 1 worker, E. O. Wilson [MCZC]; Lignumvitae Key, 1974, 7 workers, 1 soldier, R. Silberglied & E. O. Wilson [MCZC]; Plantation Key, 14.VI.1958, 6 workers, 1 soldier, 2 gynes, E. O. Wilson [MCZC].

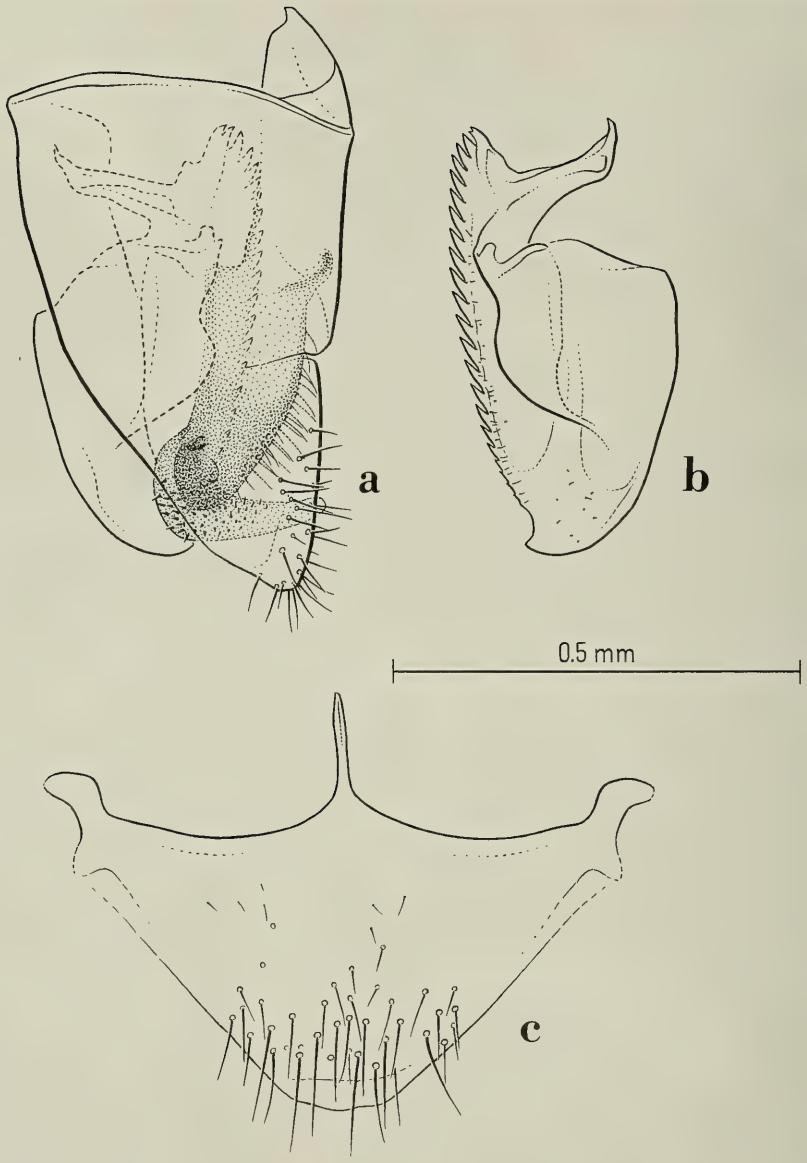


Fig. 213. *Cephalotes varians* (SMITH). Male from Cards' Point, Florida. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Bahamas: Nassau, 1918, 12 workers, W. M. MANN [USNM]; Andros Island, Little Golden Key, 19.06.1904, 10 workers, W. M. WHEELER [MCZC, MZSP]; Andros Island, May-June 1904, 14 workers, 7 soldiers, 11 gynes, W. M. WHEELER [MCZC, MHNG]; High Ridge Cay, 4 workers, 1 soldier, 3 gynes, W. M. MANN [USNM]; Mangrove Cay, Andros Island, 2 workers, 2 soldiers, W. M. MANN [USNM].

Cuba: Baraguá, 13.V.1929, 1 gyne, L. C. SCARAMUZZA [MCZC]; Pazos, 1 soldier [NHMB]; Caimito, 25.04.1911, 1 worker, KUBÉ [NHMB]; Playa Mariano, 25.05.1933, 6 workers, 1 soldier, BIERIG [MZSP]; Sierra Anafe, XII.1932, 2 workers, BIERIG [MZSP]; Cayamas, 1 worker, E. A. SCHWARTZ [MCZC]. Pinar del Río: San Vicent, VI.1953, 1 worker, E. O. WILSON [MCZC]; Sierra de los Organos, 1 worker, BIERIG [NHMB]. Isla de la Joventud (Island of Pines): Nueva Gerona, V.1923, 6 workers (2 pupae), S. C. BRUNER [USNM]. Matanzas: Cárdenas, 1 worker, W. M. MANN [MZSP]. Cienfuegos: no further locality, 1917, 18 workers, 6 soldiers, W. M. MANN [USNM]; Mina Carlota, Cumanayagua, 2 workers, 1 soldier, CREIGHTON [MCZC]; Harvard Bot. Gardens, Soledad, 03 & 09.X.1933, 1 worker, 2 soldiers, 1 gyne, N. A. WEBER [MCZC]; nr. Casa Harvard, Soledad, 21.VII, 09.VIII.1933, 7 workers, 1 soldier, 2 gynes, 1 male, N. A. WEBER [MCZC]; Atkins Gardens, Soledad, L. V., 13.VII.1953, 2 workers (nocturnal foragers), E. O. WILSON [MCZC]; Limones, Seboruco, Soledad, 03.VIII.1933, 2 workers, N. A. WEBER [MCZC]. Oriente: Yateras, 1918, 9 workers, 3 soldiers, W. M. MANN [USNM]. Santiago de Cuba: Coast below Pico Turquino, 26.VI.1936, 1 soldier [MCZC]; El Caney, 2 workers, 1 soldier, W. M. MANN [MZSP].

Discussion. - Among the material of *C. varians* examined we observed the following variation: all the specimens from the Bahamas and those from Yateras (Cuba) have shorter peduncular spines. There seems to be no evident geographic pattern in the distribution of this character. The Bahamian specimens, in addition, may have the propodeal sides with a pair of teeth of variable size or simply marginate.

According to ALAYO DALMAU (1973), in Cuba, this species is to be found over the whole island but is rare.

FERNÁNDEZ et al. (1996) report *varians* from the Colombian state of Bolívar. We cannot confirm the presence of this species in S America on the basis of the material available for the present study.

Distribution: Florida, Bahamas, Cuba.

Cephalotes jamaicensis (FOREL) new combination, new status (tentative)
Fig. 214

Cryptocerus varians var. *jamaicensis* FOREL, 1922: 97. Worker. Original description. Type locality: Kingston (Jamaica). Type material: 2 syntype workers in MHNG labelled: "Kingston, Jard. bot. (Forel), *Cryptocerus* (*Cyathocephalus*) *varians* Sm. v. *jamaicensis*, worker, type, For., *Cr.* (*Cy*) v. *jamaicensis* For.", examined.

Paracryptocerus varians (SMITH), KEMPF, 1958 a: 155, 157. Worker. Partim. Misidentification.

Diagnosis. - A member of the *pallens* clade characterised by the following apomorphies: in the worker the propodeum with a pair of narrow, membranaceous, lateral expansions, in the soldier by the head disc with contiguous foveae, by the hind femora with superficial carina, and by the head slightly broader than long.

Worker (Fig. 214). - Differing from *varians* in the following: propodeal sides with a pair of broader membranaceous expansions slightly convex and gently converging posteriorly. Gaster with a pair of anterolateral membranaceous expansions of different thickness, continuing after the stigma as a carina.

Sculpture. Foveae on the head dorsum more superficial than in *varians*, shallower on the frontal carinae. First gastral tergite with denser and deeper foveae more impressed on the anterior half.

Pilosity. As in *varians* except for the gaster where the hairs are more appressed.

Colour. Dark brown to black with slightly lighter legs.

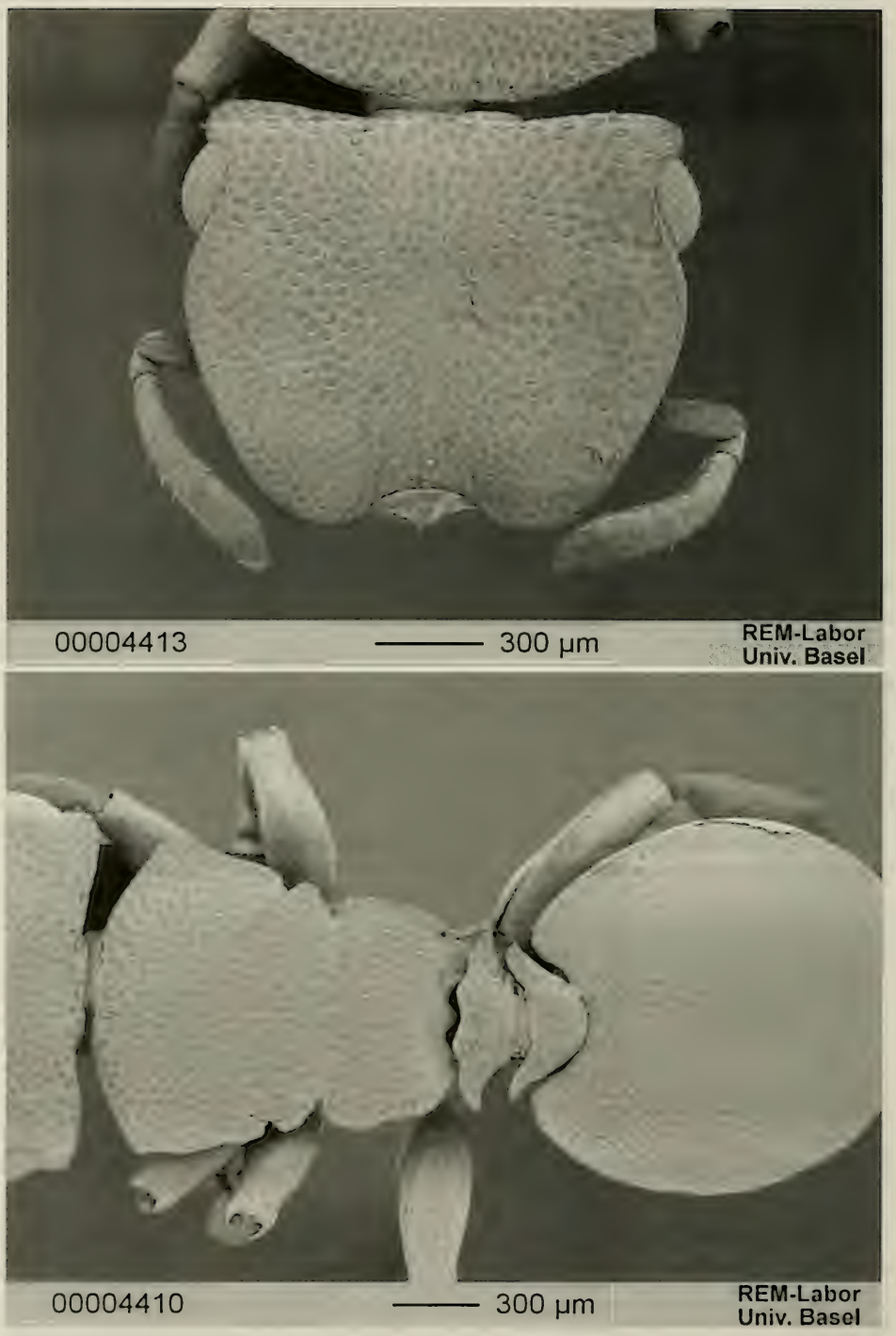


Fig. 214. *Cephalotes jamaicensis* (FOREL). Worker from Kingston, Jamaica: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 4.56–4.96; HL 1.08–1.14; HW 1.28–1.34; EL 0.27–0.30; PW 1.06–1.16; PeW 0.65–0.72; PpW 0.61–0.64; HBaL 0.35–0.38; HBaW 0.12–0.13; CI 116.1–118.5; PI 115.5–120.7; PPeI 155.6–173.1; PPpI 173.8–196.6; HBaI 34.2-35.1.

Soldier (previously undescribed). - Differing from *varians* in the following: head disc slightly broader than long, almost round. Floor of the disc more convex medially. Promesonotal suture less impressed. Sides of the basal face of the propodeum with a pair of small, triangular teeth followed by a pair of long, thick teeth strongly curved up and forwards. Declivous face of the propodeum narrowing posteriorly and with strongly carinate border.

Pedicel with well developed spines.

Gaster with a pair of strongly protruding anterior lobes.

Sculpture. Head dorsum minutely punctate, superficially shining and completely covered with large, dense, subhexagonal foveae contiguous each other. Posterior sides of the head with foveae similar to those on the head dorsum; the foveae less regular and smaller on the anterior sides of the head. Ventral part of the head reticulate, opaque and with small, slightly irregular foveae separate by short, irregular rugosities on the posterior sides and on the anterior half. Anterior third of the first gastral tergite covered by deep, oval foveae; the foveae more superficial on the remaining tergites and sternites.

Pilosity. Hairs arising from the foveae of the disc subdecumbent to decumbent and longer than in *varians*.

Colour. Black with slightly lighter legs.

Measurements (in mm) and indices: TL 6.95; HL 1.84; HW 1.90; EL 0.36; PW 1.78; PeW 0.72; PpW 0.72; HBaL 0.38; HBaW 0.15; CI 103.3; PI 106.7; PPeI 247.2; PPpI 247.2; HBaI 39.5.

Material examined. - **Jamaica:** no further locality, 1 worker [USNM]; Kingston, Botanical Garden, 2 workers (syntypes), FOREL [MHNG]; same locality, 30.V.1941, 1 worker, 1 soldier, E. A. CHAPIN [USNM]; Half Way Tree, 28.I.1937, 4 workers, E. A. CHAPIN & BLACKWELDER [MCZC, MZSP].

Discussion. - KEMPF (1958 a) considered *jamaicensis* as a straight synonym of *varians*. As a matter of fact, the workers of *jamaicensis* resemble in the propodeal and head shapes the large workers of *varians* from Yateras and Cienfuegos (Cuba). The small differences in microsculpture and propodeal morphology emphasised in our description may be regarded as sufficient to separate the two species.

KEMPF (l. c.), however, did not see any soldiers referable to *jamaicensis*. The unique soldier from Jamaica available for the present study differs from all the other *varians* soldiers examined by having the foveae of the head disc larger and contiguous on the whole disc (more spaced and absent on the border of the disc in *varians*). In addition, each fovea bears a subdecumbent or decumbent hair slightly longer than in *varians*. Other characters separating *jamaicensis* from *varians* in the soldier caste are the propodeal and pedicellar spines much larger in *jamaicensis*. In spite of the sole soldier studied, *jamaicensis* is likely to have an obvious biogeographic meaning as a Jamaican endemic and we propose to consider it a good species at least until true transitional forms with *varians* will be discovered.

Distribution: Jamaica.

Cephalotes patellaris (MAYR) new combination, bona species
Figs. 215, 216, 217

Cryptocerus patellaris MAYR, 1866 b: 907, pl. 20, fig. 15. Gyne. Original description. Type locality: Brazil. Type material: holotype gyne (dealate) labelled "Brasil, F. Sahlli, *Cryptocerus patellaris*, Typ., Mayr" in NHRS, examined.

Paracryptocerus pallens (KLUG), KEMPF, 1958: 151. Partim. Nec KLUG, 1824. Misidentification.

Diagnosis. - A member of the *pallens* clade characterised by the following apomorphies: in the worker the propodeum with broad, strongly crenulate membranaceous expansions, petiolar spines 1.3 times longer than the maximum petiolar length; in the soldier and in the gyne by the head disc with spaced foveae, by the foveal hairs suberect; in the soldier only by the hind femora strongly carinate; and, in the gyne only, by the almost round head.

W o r k e r (Fig. 215) (previously undescribed). - Similar to the other species of the group from which it differs for one or more of the following characters. Head broader than long. Frontal carinae with minutely crenulate border in some specimens. Membranaceous expansions of the vertexal angles broad and crenulate. Pronotal sides with a pair of broad, membranaceous expansions with crenulate borders, the crenulation stronger in larger specimens. Mesonotal sides with a pair of triangular, membranaceous teeth generally rounded; some specimens with an additional pair of minute denticles. Propodeal sides with a pair of broad, membranaceous expansions broadening posteriorly. Anterior border of the petiole concave and with a salient pair of swellings. Petiolar sides with a pair of pointed spines slightly longer than their maximum length. Postpetiolar sides with a pair of pointed spines directed forwards. Gaster oval and with a pair of broad, anterolateral membranaceous expansions surpassing the stigma posteriorly and continuing to the posterior border of the first tergite as a marked margin. Hind and mid femora angulate; their distal part with a dorsal longitudinal crest much narrower on the mid femora. Mid and hind basitarsi flat, with the proximal part broader than the distal one.

Sculpture. Head dorsum and mesosoma minutely reticulate-punctate with superimposed deep, dense foveae, smaller and less regular on the frontal carinae; some specimens with additional oblique, thin rugosities on the frontal carinae. Ventral part of the head reticulate and with small, irregular foveae on the anterior half; some specimens with additional irregular, longitudinal rugosities on the whole ventral part of the head. Pedicel minutely reticulate-punctate and with dense, small, slightly irregular foveae. Pleurae strongly reticulate and with thin, longitudinal rugosities. Anterior third of the first gastral tergite strongly reticulate and with superficial, irregular foveae separate by longitudinal rugosities; similar sculpture on the remaining first gastral tergite but less impressed. Gastral sternites strongly reticulate and with thin, slightly irregular rugosities. Legs strongly reticulate and with minute, superficial, foveae, more impressed and denser on the outer face of the tibiae, larger on the dorsum of the fore femora; some specimens with short, longitudinal rugosities on the posterior face of the hind femora.

Pilosity. Body foveae with appressed hairs, sometimes decumbent on the head. Frontal carinae, vertexal angles, and, to a lesser extent, dorsum of the first gastral tergite, and legs with thick clubbed hairs. Posterior border of the remaining gastral segments with hairs slightly thinner and longer than those on the border of the frontal carinae. Gastral sternites with additional, rare, long, pointed hairs.

Colour. Brown to black with the frontal carinae and the membranaceous expansions of the body slightly lighter.

Measurements (in mm) and indices: TL 3.74–5.14; HL 0.85–1.14; HW 0.99–1.36; EL 0.22–0.30; PW 0.80–1.22; PeW 0.58–0.77; PpW 0.56–0.70; HBaL 0.23–0.32; HBaW 0.10–0.14; CI 116.5–119.3; PI 111.5–123.7; PPeI 137.9–155.4; PPpI 142.8–174.3; HBaI 43.5–43.7.

S o l d i e r (Fig. 216) (previously undescribed). - Head disc suboval, slightly longer than broad. Border of the disc strongly raised and with the posterior half with minutely crenulate margin. Floor of the disc medially with a pointed tumulus. Vertex with a superficial depression.

Mesosoma. Humeral angles with a pair of obtuse, semi-membranaceous teeth. Pronotal sides gently converging posteriorly. Pronotal carina well marked, with variably crenulate margin and shortly interrupted medially. Mesonotal sides with a pair of broad, triangular teeth, or with almost round tip and with an additional pair of minute denticles in some specimens. Propodeum with differentiate basal and declivous faces; sides of the basal face superficially notched or gently convex and followed by a pair of short, stout teeth curved upwards in large specimens; small specimens with narrow membranaceous expansions only.

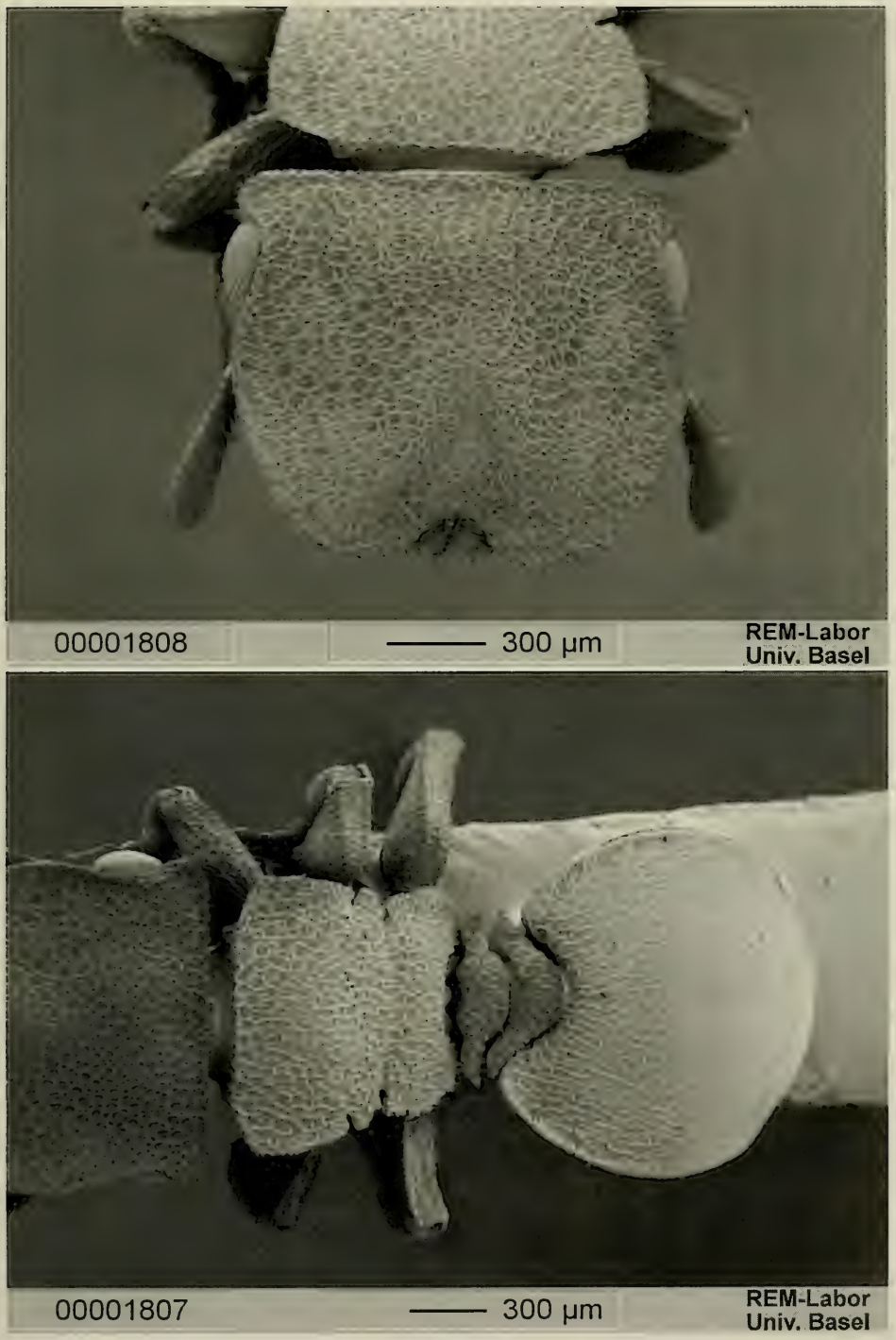


Fig. 215. *Cephalotes patellaris* (MAYR). Worker from Ilha da Vitória (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Pedicel as in the worker but with narrower and shorter spines.

Mid and hind femora dorsally angulate and with a pair of distal carinae stronger on the hind femora. Mid and hind basitarsi flat, broader proximally than distally.

Gaster oval and with a pair of protruding lobes.

Sculpture. Head dorsum minutely punctate, variably shining and with large foveae, smaller on the tumulus and sparse to rare on the frontal carinae; the foveae denser almost on the whole disc in small specimens. Sides of the head disc punctate, densely and irregularly foveolate-rugulose, the foveae diminishing in size anteriorly. Ventral part of the head punctate, variably shining and covered by irregular, longitudinal rugosities and foveae. Vertexal angles and mesosoma minutely reticulate-punctate and with dense foveae, larger on the vertexal angles and on the pronotum. Pedicel with sculpture similar to the one on the propodeum but with smaller foveae. Pleurae strongly reticulate; propleurae longitudinally irregularly foveolate-rugose, the rugae slightly transversal in some specimens; meso- and metapleurae with small, shallow, sparse foveae and few, longitudinal, thin rugosities, the foveae rare on the metapleurae. Gaster and legs with sculpture similar to the one of the worker; large specimens with the gaster covered by deep longitudinal rugosities.

Pilosity. Each fovea on the head dorsum with a suberect hair; those on the remaining body parts with an appressed or decumbent hair. Borders of the disc and sides of the head with many suberect, long, clavate hairs, shorter on the antero-ventral part of the disc. Pronotum, gaster and legs with rare, clubbed hairs. Parts of the gaster and legs without foveae with short, appressed, thin hairs. Gastral sternites with additional rare, long, pointed hairs.

Colour. Dark brown to black.

Measurements (in mm) and indices: TL 6.55–7.40; HL 1.68–1.96; HW 1.72–1.88; EL 0.34–0.36; PW 1.72–1.86; PeW 0.76–0.86; PpW 0.73–0.83; HBaL 0.33–0.37; HBaW 0.14–0.15; CI 95.9–102.4; PI 100.0–101.1; PPeI 216.3–226.3; PPpI 224.1–235.6; HBaI 40.5–42.4.

G y n e (Fig. 217). - Differing from the soldier in the following details.

Head more round. Sides of the disc with the borders slightly lower and with the margin more crenulate. Vertex with deeper median depression.

Mesosoma. Humeral angles with a pair of short, triangular teeth or simply obtuse. Pronotal carina lower. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly convex and posteriorly with a small pair of teeth with or pointed tip and slightly diverging laterally.

Petiole. Anterior face oblique and slightly concave. Petiolar sides with a pair of pointed denticles. Postpetiole convex dorsally and with broad lateral spines with truncate apex and pointed backwards.

Gaster. Similar to that of the soldier but much longer.

Legs with less impressed carinae on the outer face of the femora.

Sculpture. Foveae of the head dorsum larger than in the soldier and often denser. Mesonotal foveae slightly shallower. Foveae on the basal face of the propodeum smaller. Pleurae reticulate. Propleurae with thin, superficial, slightly longitudinal rugosities. Border of the lower metapleurae with thin, longitudinal rugosities. Upper part and center of the lower mesopleurae with small foveae, deeper and denser on the upper mesopleurae.

Pilosity. As in the soldier except for the clubbed hairs thinner, longer and more abundant on the gaster and on the legs and also present on the whole mesosoma and on the pedicel.

Colour. Dark brown to black.

Measurements (in mm) and indices: TL 8.36–9.04; HL 1.68; HW 1.60–1.64; EL 0.35–0.36; PW 1.56–1.60; PeW 0.68–0.71; PpW 0.79–0.83; HBaL 0.44–0.46; HBaW 0.18–0.20; CI 95.2–97.6; PI 100.0–105.1; PPeI 219.7–235.3; PPpI 187.9–202.5; HBaI 40.9–43.5.

M a t e r i a l e x a m i n e d . - **Brazil**: no further locality, 1 gyne (holotype), F. SAHLLI [NHRS]. M i n a s G e r a i s : Pedra Azul, 19.XI.1972, 800 m, 1 gyne, SEABRA & ALVARENGA [MZSP]; Serra do Cipó, 07.VII.1974, 1 gyne, C. G. FROEHLICH [MZSP]; Manhumirim, 17.IV.1962, 1 worker, 1 gyne, F. M. OLIVEIRA [MZSP]. S ã o P a u l o : São Roque, 25.XII.1971, 1 worker, 1 gyne, F. LANE [MZSP]; São Sebastião, 06.III.1958, 15 workers, 3 soldiers, W. W. KEMPF [MCZC]; Ilha da Vitória, 29.III–06.IV.1965, 71 workers, 17 soldiers, Exp.

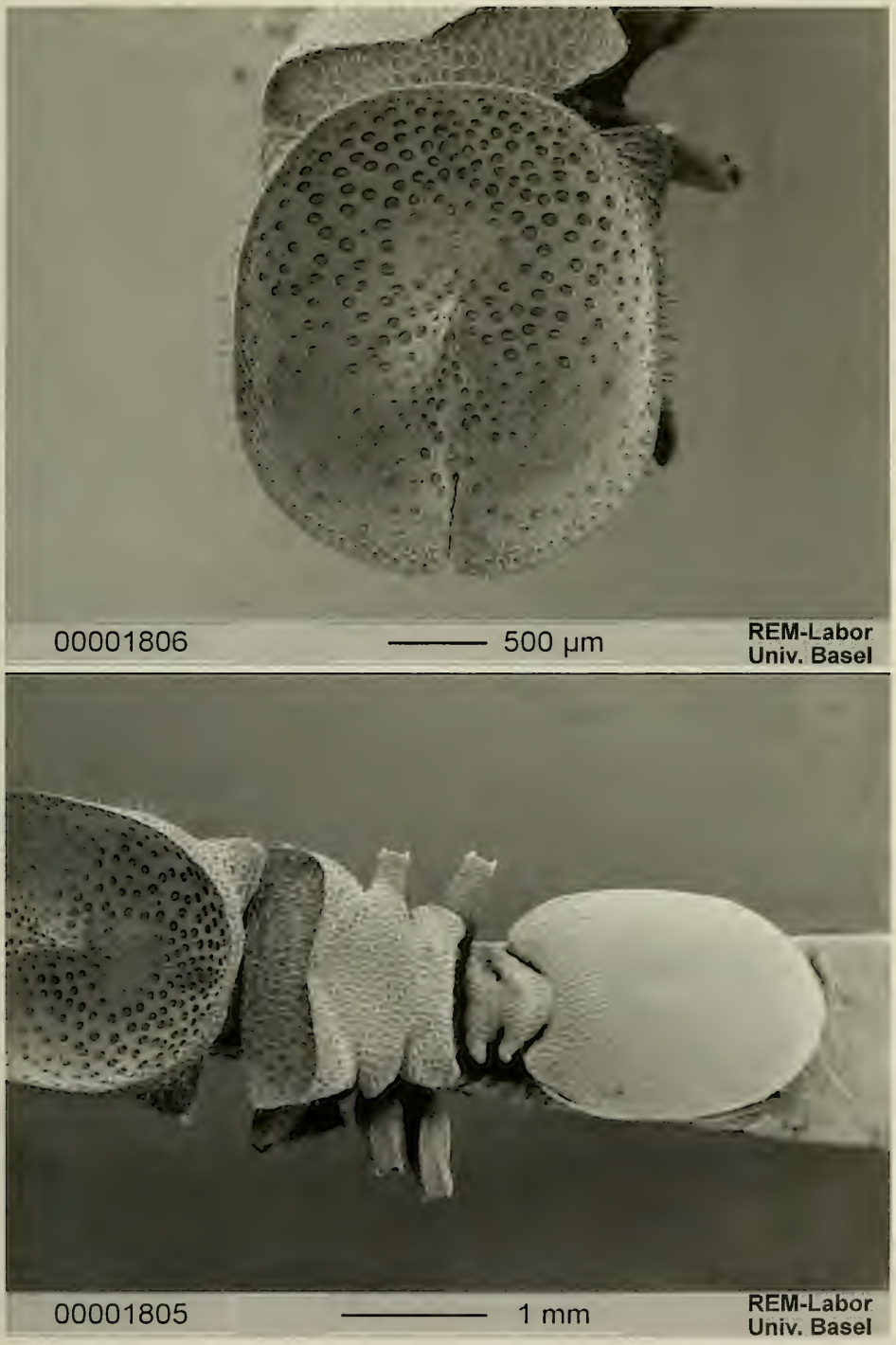


Fig. 216. *Cephalotes patellaris* (MAYR). Soldier from Ilha da Vitória (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

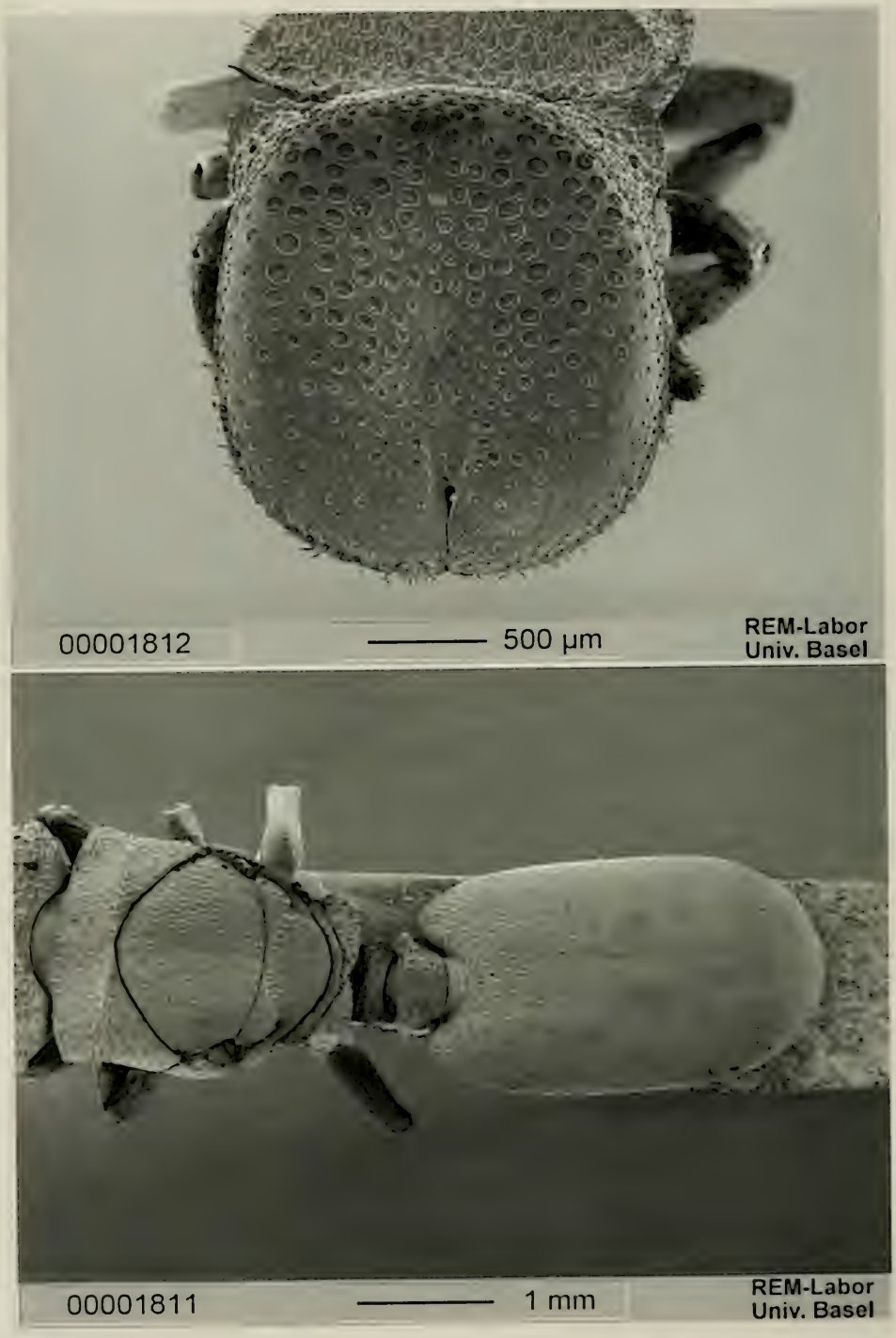


Fig. 217. *Cephalotes patellaris* (MAYR). Gyne from Pedra Azul (Minas Gerais), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Dep. Zool. [MZSP]; Ilha dos Búzios, 16.X.1963, 1 worker, Exp. Dept. Zool. [MZSP]. Rio de Janeiro: Rio de Janeiro, 21.XII.1927, 1 soldier, O. CONDE; Represa Rio Grande, Guanabara, 14–17.XI.1960, 1 soldier, F. M. OLIVEIRA [MZSP]. Santa Catarina: Nova Teutônia, 27°11' B, 52°23' L, 300–500 m, 1 worker, 6 soldiers, F. PLAUMANN [MCZC, MZSP]; same locality, IX.1936, 1 worker, F. PLAUMANN [MZSP]; same locality, XII.1959, X.1971, X.1973, 4 workers, 2 soldiers, F. PLAUMANN [MZSP]; Rio Grande do Sul: Pareci Novo, 22 & 26.VI, 25.VII.1927, 32 workers, 7 soldiers, S. J. HANSEN [MZSP]; Porto Alegre, 02.XII.1930, 2 workers, 2 soldiers, P. BUCK [MZSP].

Discussion. - EMERY (1894 a), who had the type of this species examined for him by Prof. Aurivillius, maintained *patellaris* as a variety of *pallens* on the basis of the complete anterior junction of the disc (incomplete in *pallens*). KEMPF (1958 a) synonimysed *C. patellaris* with *pallens* without having seen the unique type in Stockholm since the material available to him showed extensive variation in this character. We confirm the irrelevant taxonomic value of the anterior junction of the disc but the holotype of MAYR agrees with other gynes from different Brazilian localities. All these gynes plus the workers and soldiers associated with them differ from the true *pallens* by the characters already listed in the diagnosis. *Patellaris*, hence, represents a valid species, apparently a southern vicariant of the true *pallens*.

Distribution: Brazil.

Cephalotes pallidus DE ANDRADE new species
Figs. 218, 219, 220, 221, 390

Paracryptocerus pallens (KLUG), KEMPF, 1958 a: 151. Partim. Nec KLUG, 1824. Misidentification.

Zacryptocerus pallens, WHEELER & HÖLLDOBLER, 1985: 338, figs. 4–6. Soldier. Misidentification.

Type material: Holotype soldier from Guyana labelled: Kartabo, B. G. Jul. Aug. 1920, W. M. Wheeler [MCZC]. Paratypes: 27 workers and 15 soldiers, same data as the holotype [MCZC, MZSP].

Derivatio nominis: in Latin *pallidus* has the same meaning as *pallens*, the name of one of the species with which the present had been previously confused.

Diagnosis. - A member of the *pallens* clade differing from its sister species, *pallidoides*, by the following characters: in the worker, soldier and gyne, body sculpture deeper, femora less inflate, and HBaI $\leq$ 48, and, in the soldier and gyne only, floor of the disc with a protruding swelling and margin of the disc more densely crenulate.

Worker (Fig. 218). - Similar to the other species of the group from which it differs for one or more of the following characters. Head broader than long. Membranaceous expansions of the vertexal angles variably developed and strongly crenulate. Frontal carinae crenulate.

Mesosoma. Pronotum with a pair of developed membranaceous expansions. Mesonotum with a pair of triangular or truncate teeth. Propodeum with a pair of broad, gently convex, crenulate, membranaceous expansions, the crenulations variably impressed according to the specimen.

Anterior face of the petiole slightly concave. Petiolar sides with a pair of pointed spines more than 1.3 longer than the maximum petiolar length. Postpetiolar sides with a pair of pointed spines shorter than those of the petiole and directed forwards.

Gaster oval and with a pair of protruding membranaceous expansions reaching the stigma posteriorly and continuing as a thin margin backwards up to the posterior border.

Mid and hind femora gently angulate; mid femora with a carina; hind femora with a crest. Mid and hind basitarsi flat, with the proximal part much broader than the distal one.

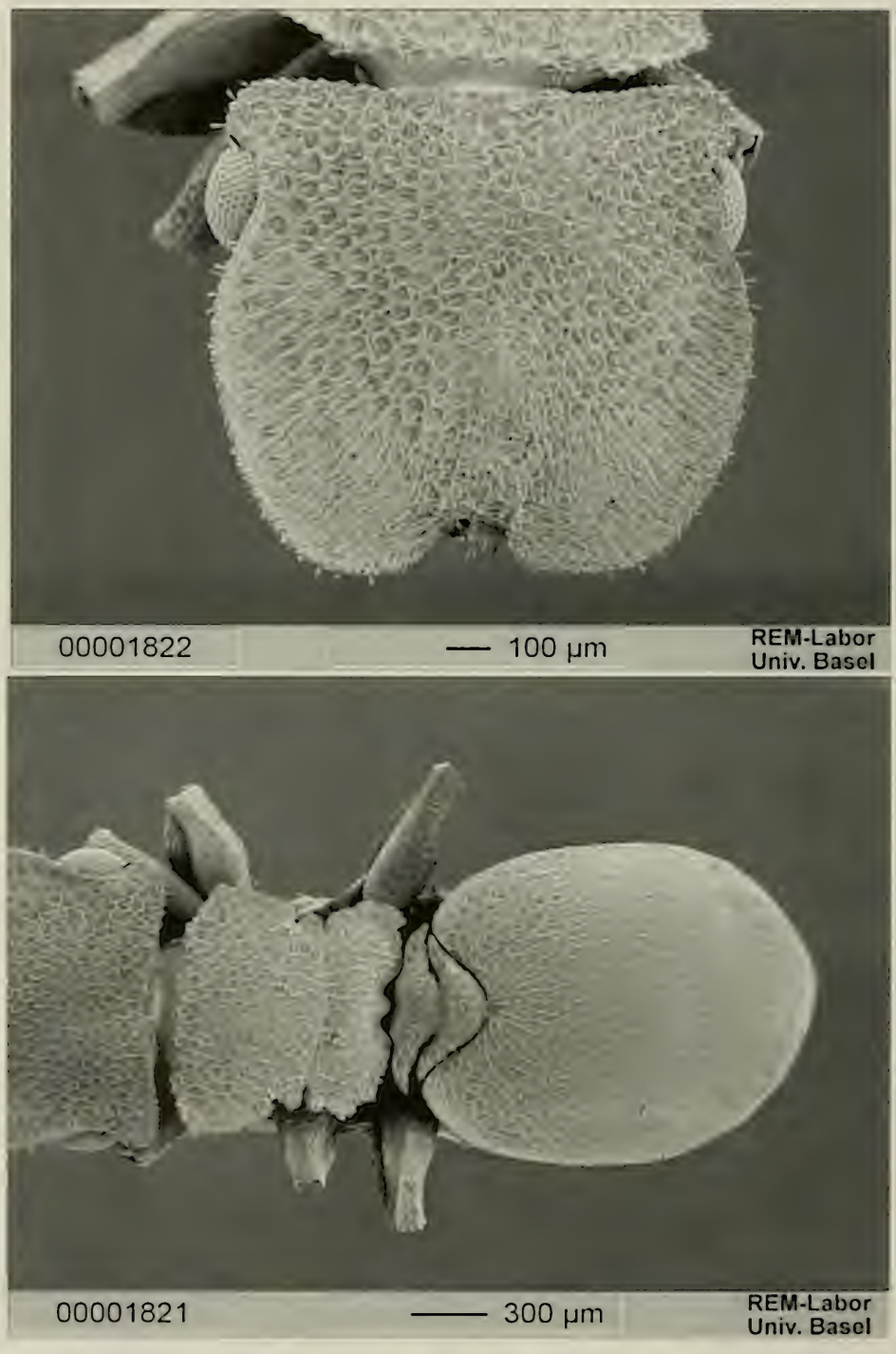


Fig. 218. *Cephalotes pallidus* DE ANDRADE. Worker from Belém (Pará), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Sculpture. Head dorsum minutely punctate, with dense, deep, irregular foveae diminishing in size anteriorly, sparser or rare and more superficial on the frontal carinae. Frontal carinae with strong, oblique rugosities. Ventral part of the head strongly reticulate. Mesosoma minutely punctate and with dense foveae as on the head dorsum, the foveae smaller on the mesonotum and on the propodeum. Propodeum with additional, irregular, longitudinal rugosities. Pleurae usually strongly reticulate, only with superficial, irregular, sparse foveae and few, thin rugosities in some specimens. Pedicel punctate and with small, dense, irregular foveae. Anterior third and sides of the first gastral tergite strongly reticulate and with superficial, irregular foveae; the foveae diminishing in size posteriorly and separate by thin, irregular, longitudinal rugosities only on the anterior third. First gastral sternite strongly reticulate and with irregular, thin rugosities. Remaining gastral tergites and sternites reticulate. Legs strongly reticulate and with small, irregular foveae, dense on the outer face of the tibiae.

Pilosity. Each fovea with a decumbent hair. Sides of the frontal carinae, of the vertexal angles, first gastral tergite, posterior borders of the gastral segments and legs with short, clubbed hairs, denser on the sides of the frontal carinae. Gastral sternites with two additional types of erect, pointed hairs: (1) sparse and short and, (2) rare, long and thin on the second sternite. Parts of the gaster and legs without foveae simply with appressed, thin hairs.

Colour. Brown to black with the membranaceous expansions of the body lighter.

Measurements (in mm) and indices: TL 3.97–4.49; HL 0.96–1.02; HW 1.04–1.16; EL 0.25–0.26; PW 0.90–1.00; PeW 0.63–0.72; PpW 0.52–0.61; HBaL 0.23–0.28; HBaW 0.11–0.12; CI 108.3–114.0; PI 114.0–122.1; PPeI 138.9–142.8; PPpI 161.0–173.1; HBaI 42.3–47.8.

S o l d i e r (Figs. 219, 390). - Head longer than broad. Sides of the disc raised and with strongly crenulate margin. Floor of the disc with a convex median tumulus pointed apically in large specimens. Vertex posteriorly variably depressed. Vertexal angles with crenulate margin.

Mesosoma. Humeral angles with a pair of obtuse, semi-membranaceous teeth. Pronotum gently converging posteriorly. Pronotal carina marked, crenulate and shortly interrupted medially, continuous and simply lower in the middle in some specimens. Mesonotum with a pair of broad, round or truncate teeth. Sides of the basal face of the propodeum with one-two pairs of irregular swellings followed by a pair of stout teeth curved upwards and forwards. Declivous face of the propodeum narrowing posteriorly narrowly marginate in small specimens.

Anterior face of the petiole medially concave. Petiolar and postpetiolar sides with spines shorter and less pointed than in the worker.

Gaster oval with a pair of protruding lobes.

Mid and hind femora dorsally gently angulate and with a distal carina; the carina more impressed on the hind femora.

Sculpture. Head dorsum minutely punctate and with deep, large, irregular, contiguous foveae; some specimens with the foveae less regular and separate by oblique rugosities. Internal border of the disc strongly punctate occasionally superimposed to irregular, short rugosities. Floor and sides of the disc often completely covered by a thick layer of probable camouflage material; when uncovered the internal surface of the disc shining. Sides of the disc densely and irregularly foveolate-rugulose, more superficially on the anterior half. Ventral part of the head shining, punctate and with irregular longitudinal rugosities. Mesosoma punctate and with dense, irregular foveae. Pedicel with sculpture similar to the one on the mesosoma but the foveae shallower and smaller. Pleurae reticulate and with superimposed irregular foveae on the dorsal half of the propleurae and upper border of the metapleurae; rugosities between the foveae in large specimens only. Gaster and legs with sculpture similar to the worker.

Pilosity. Foveae on the head dorsum with a suberect, slightly clubbed hair; those on the mesosoma, pedicel, gaster and legs with an appressed or decumbent hair. Borders of the disc and foveae on the sides of the head with erect, long, clavate hairs. Vertexal angles, pronotum, pedicel, gastral tergites and legs with rare, clubbed hairs. First gastral sternite with pointed hairs similar to those of the worker. Body parts without foveae with sparse, appressed, thin, short hairs.

Colour. Brown to black.

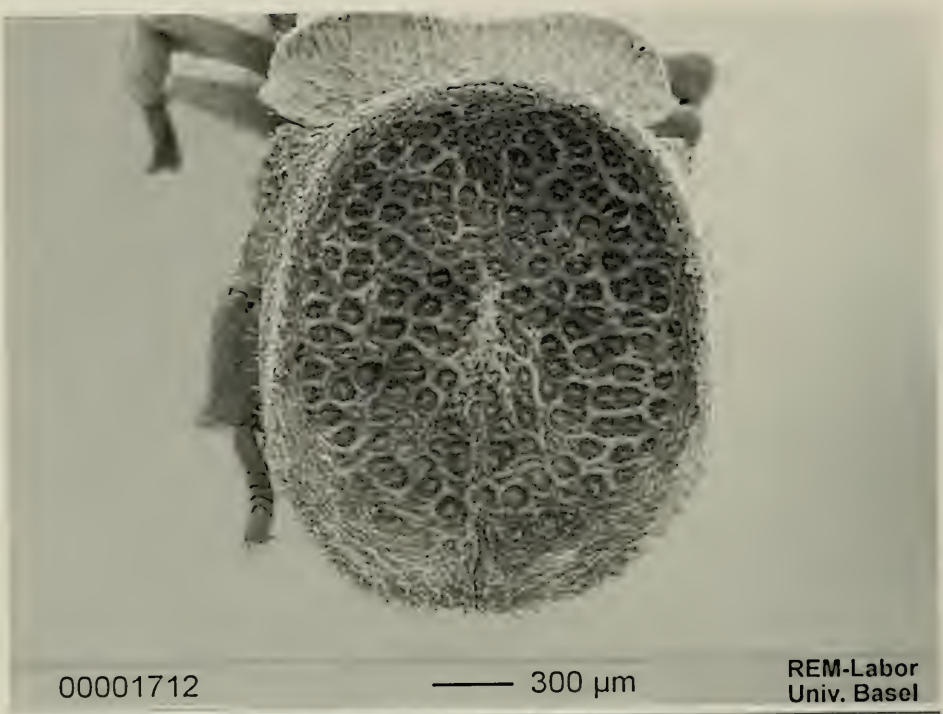


Fig. 219. *Cephalotes pallidus* DE ANDRADE. Soldier from Reyes, Bolivia: head (top) and meso- and metasoma (bottom) in dorsal view.

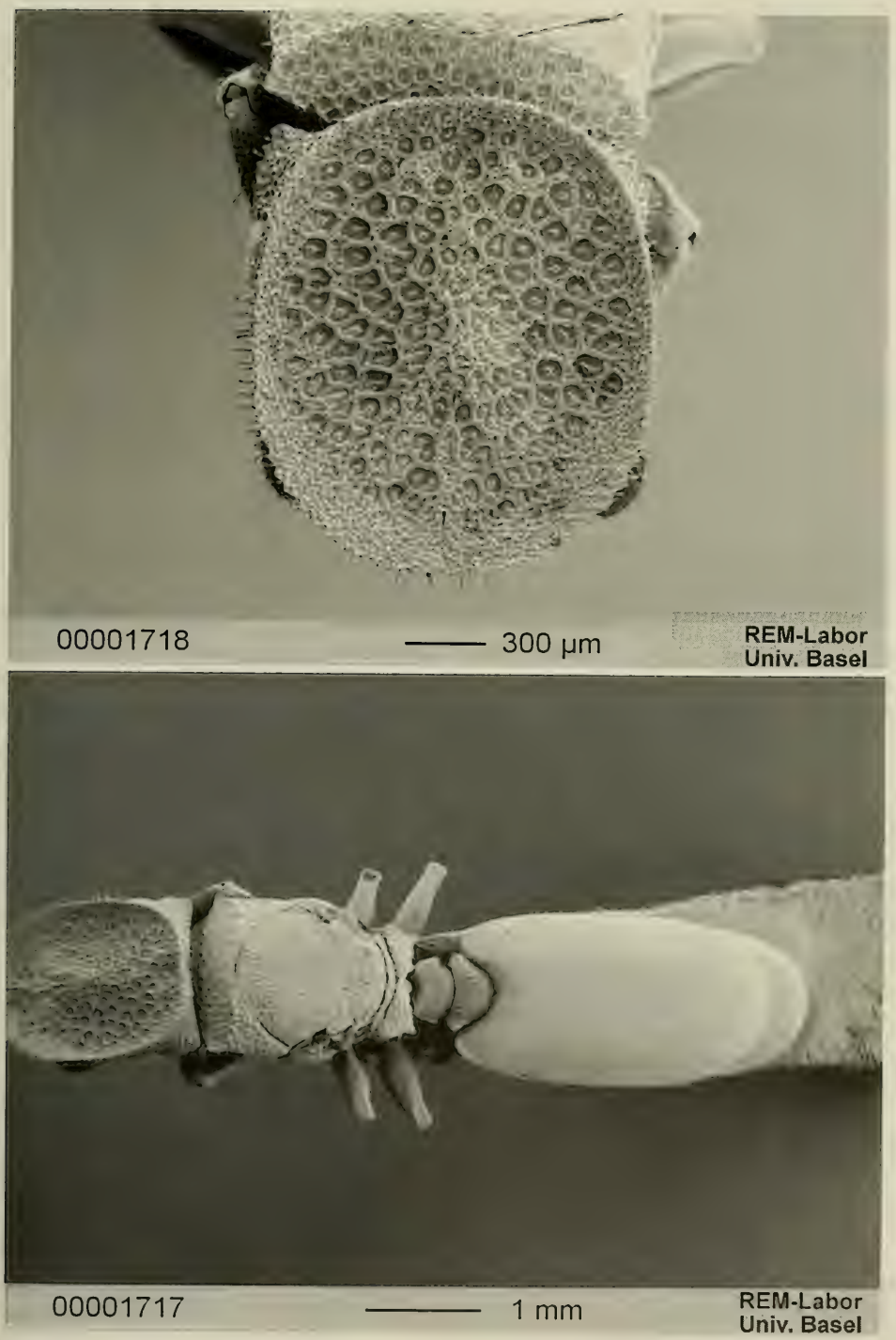


Fig. 220. *Cephalotes pallidus* DE ANDRADE. Gyne from Belém (Pará), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 5.08–6.87; HL 1.40–1.88; HW 1.30–1.64; EL 0.30–0.31; PW 1.24–1.56; PeW 0.63–0.69; PpW 0.55–0.67; HBaL 0.26–0.32; HBaW 0.12–0.14; CI 87.2–92.8; PI 104.8–109.4; PPeI 196.8–226.1; PPpI 225.4–232.8; HBaI 43.7–48.1.

G y n e (Fig. 220). - Differing from the soldier in the following characters. Sides of the disc with lower border. Median depression on the vertex deeper.

Mesosoma. Humeral angles obtuse. Pronotal carina less evident and lower. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly convex and posteriorly with a pair of teeth slightly diverging externally and separate by a deep incision.

Anterior face of the petiole oblique and gently concave medially. Petiolar sides with a pair of small denticles. Postpetiole convex; its sides with a pair of broad, short spines pointed posteriorly.

Gastral anterior lobes more developed.

Legs as in the soldier.

Sculpture. As in the soldier but the transversal rugosities on the floor of the disc are unknown. Foveae on the propodeum smaller. Upper and center of the lower mesopleurae with dense, small foveae, more regular on the upper mesopleurae.

Pilosity. As in the soldier except for the clubbed hairs on the pedicel, on the gaster, on the legs and on the mesosoma, slightly denser.

Colour. As in the soldier.

Measurements (in mm) and indices: TL 7.32–7.72; HL 1.52; HW 1.40–1.42; EL 0.36; PW 1.32–1.42; PeW 0.54–0.60; PpW 0.66–0.72; HBaL 0.38–0.40; HBaW 0.15–0.18; CI 92.1–93.4; PI 100.0–106.1; PPeI 237.5–244.4; PPpI 183.7–215.1; HBaI 39.5–45.0.

M a l e . - Similar to the other species of the group from which it differs for one or more of the following characters. Frontal carinae strongly raised and convex. Clypeus gently convex posteriorly and not incised anteriorly. Pronotum in dorsal view with traces of scapular angles.

Genitalia and subgenital plate as in Fig. 221.

Sculpture. Head dorsum minutely reticulate, irregularly foveolate-rugose, the rugae oriented transversally in front of the eyes and between the scapes. Ventral part of the head reticulate; its posterior sides rugulose-foveolate, the rugae oblique and the foveae small; ventral part of the head medially with longitudinal rugosities. Pronotum minutely reticulate and with foveae separate by few, thin rugosities on the sides. Mesonotum slightly shining and with minute, superficial reticulation and with superficial, sparse foveae, the reticulation more impressed and the foveae smaller on the posterior part, both structures superimposed by thin, longitudinal rugosities. Scutellum with sculpture similar to the one on the posterior part of the mesonotum but with denser rugosities. Basal face of the propodeum reticulate and longitudinally rugulose. Propleurae reticulate. Mesopleurae superficially reticulate and with thin, longitudinal rugosities on the posterior half, covered by superficial foveae on the center of the lower and of the upper mesopleurae. Metapleurae reticulate and irregularly rugose; the rugosities oriented longitudinally on the lower part. Pedicel superficially reticulate and with thin rugosities on the sides. Gaster superficially reticulate and shining.

Pilosity as in the other species of the group.

Colour. Black. Coxae, proximal part of the femora, pedicel and gaster brown. Legs dark yellow with darker tarsomeres.

Measurements (in mm) and indices: TL 5.04; HL 0.74; HW 0.88; EL 0.35; PW 0.88; PeW 0.35; PpW 0.37; HBaL 0.46; HBaW 0.07; CI 118.9; PI 100.0; PPeI 251.4; PPpI 237.8; HBaI 15.2.

M a t e r i a l e x a m i n e d . - **Guyana**: Kartabo, Jul. -Aug. 1920, 27 workers (paratypes), 16 soldiers (holotype and paratypes), W. M. WHEELER [MCZC, MZSP].

Surinam: no further locality, 1 gyne [MCSN].

Brazil: A m a z o n a s : BR–174, km 44, 25.II.1983, 3 workers, 3 soldiers, A. Y. HARADA [INPA]; High Falls, Rio Tarumã, 30.VIII.1962, 1 worker, 1 male, W. L. BROWN [MCZC]; Ig. Marianil, Rio Branco Road, 24 km NE of Manaus, 12.IX.1962, 2 workers, W. L.

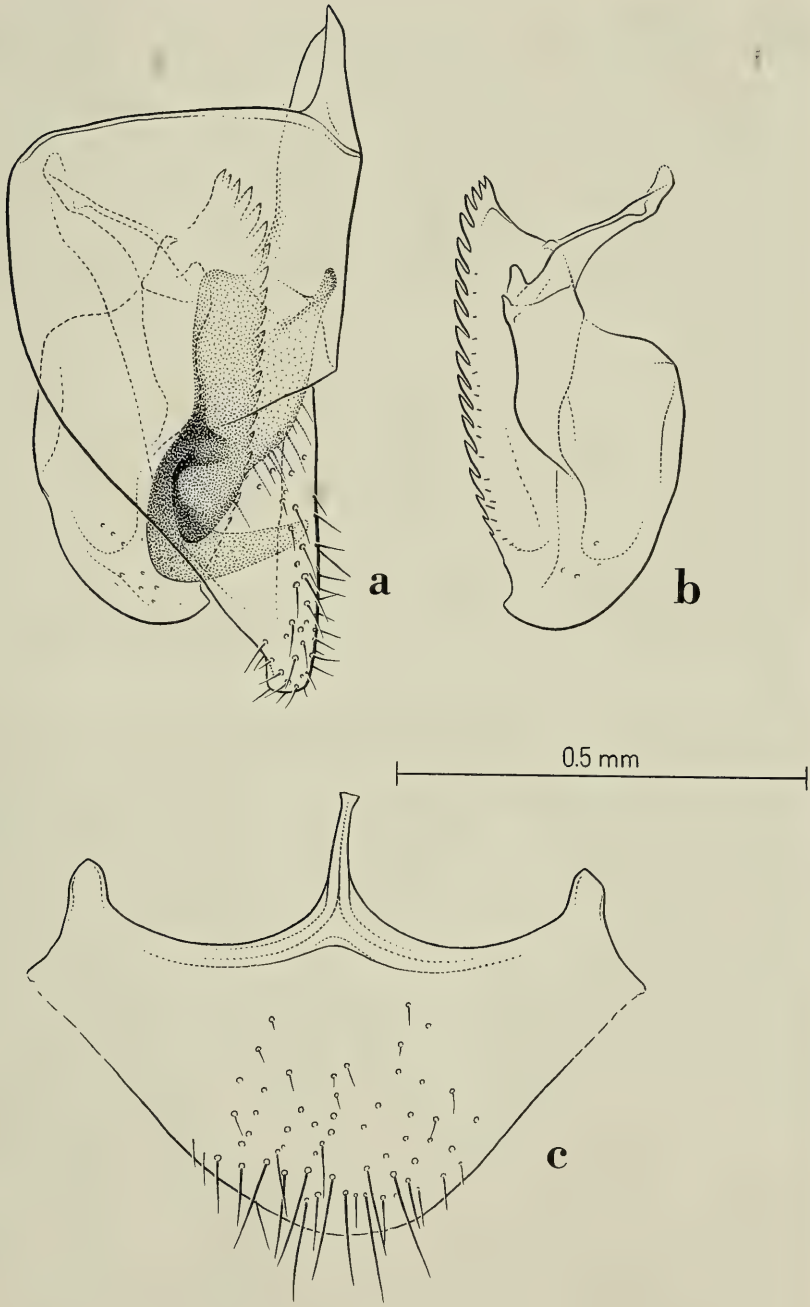


Fig. 221 *Cephalotes pallidus* DE ANDRADE. Male from High Falls, Rio Tarumã (Amazonas), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

BROWN [MCZC]. Pará: Belém, 12–19.VIII.1962, 47 workers, 3 gynes, K. LENKO [MZSP]; Primavera, Quatipuru, Fazenda Feitoria, 27–28.XI.1992, 4 workers, J. DIAS [MPEG]; São João de Pirabas, Japerica, 20–22.XII.1992, 1 worker, J. DIAS [MPEG]. Bahia: Santo Amaro, ESOMI, 13.I.1988, 1 gyne, E. FERRAZ [CPCC]. Rio de Janeiro: Silva Jardim, VIII.1974, 1 soldier, F. M. OLIVEIRA [MZSP].

Peru: Madre de Dios: Río Tambopata Reserva, 13 km SW Puerto Maldonado, 290 m, 3 workers, T. L. ERWIN [MCZC].

Bolivia: Beni: Reyes, Oct. 1921–1922, 1 worker, 1 soldier, 1 gyne, W. M. MANN [MZSP].

Discussion. - The soldier and the gyne of *pallidus* are different from all the other species of the *pallens* clade by the deep, broad, contiguous, irregular foveae on the head disc.

We listed under this species part of the *pallens* specimens identified by KEMPF (1958 a) after re-study of the material examined by him as listed above.

The statement of misidentification of the *pallens* referred by WHEELER & HÖLLDOBLER (1985) is equally based on examination of their material.

Distribution: Guyana, Surinam, Brazil, Peru and Bolivia.

Cephalotes pallidoides DE ANDRADE new species

Figs. 222, 223, 224

Cryptocerus varians SMITH, WEBER, 1938: 502. Nec SMITH, 1876. Misidentification.

Paracryptocerus pallens (KLUG), KEMPF, 1958 a: 152, pl. 8 fig. 5 and 6. Worker and soldier. Partim. Nec KLUG, 1824. Misidentification.

Type material: Holotype soldier from Brazil labelled: Utiariti (325 m), Rio Papagaio, Mato Grosso, Brasil, VII.1961, K. Lenko. Paratypes: 8 workers, 1 male, same data as the holotype, all MZSP.

Derivatio nominis: *pallidoides* is a neologism indicating the close relationship between this species and *pallidus*.

Diagnosis. - A member of the *pallens* clade differing from its sister species *pallidus* by the following apomorphies: in the worker, soldier and gyne, sculpture less impressed, femora more inflate, and HBaI $\geq$ 50, and, in the gyne only, disc with shallower and more regular foveae.

Worker (Fig. 222). - The characters listed below should allow an exhaustive differential comparison with *pallidus*.

Border of the frontal carinae and of the membranaceous expansions of the mesosoma weakly crenulate. Femora much more incrassate. Mid and hind femora angulate. Mid and hind basitarsi flat, shorter and broader.

Sculpture. Head and mesosoma with shallower foveae, dense or sparse on the frontal carinae, with thin rugosities between the foveae in some specimens only. Ventral part of the head with or without small, irregular foveae separate by short, longitudinal rugosities. Propodeum and pleurae without longitudinal rugosities. Anterior third and sides of the first gastral tergite with shallower foveae. First gastral sternite and legs with more superficial reticulation and foveae.

Pilosity. As in *pallidus* but with the hairs on the border of the frontal carinae sparser and thinner some specimens with less short, erect, pointed, hairs on the gastral sternites.

Colour. Brown to black with the membranaceous expansions lighter.

Measurements (in mm) and indices: TL 3.79–4.44; HL 0.90–1.00; HW 1.00–1.20; EL 0.23–0.26; PW 0.90–1.02; PeW 0.65–0.77; PpW 0.53–0.70; HBaL 0.20–0.26; HBaW 0.11–0.13; CI 111.1–122.2; PI 111.1–123.9; PPeI 124.3–147.8; PPpI 140.0–192.4; HBaI 50.0–61.9.

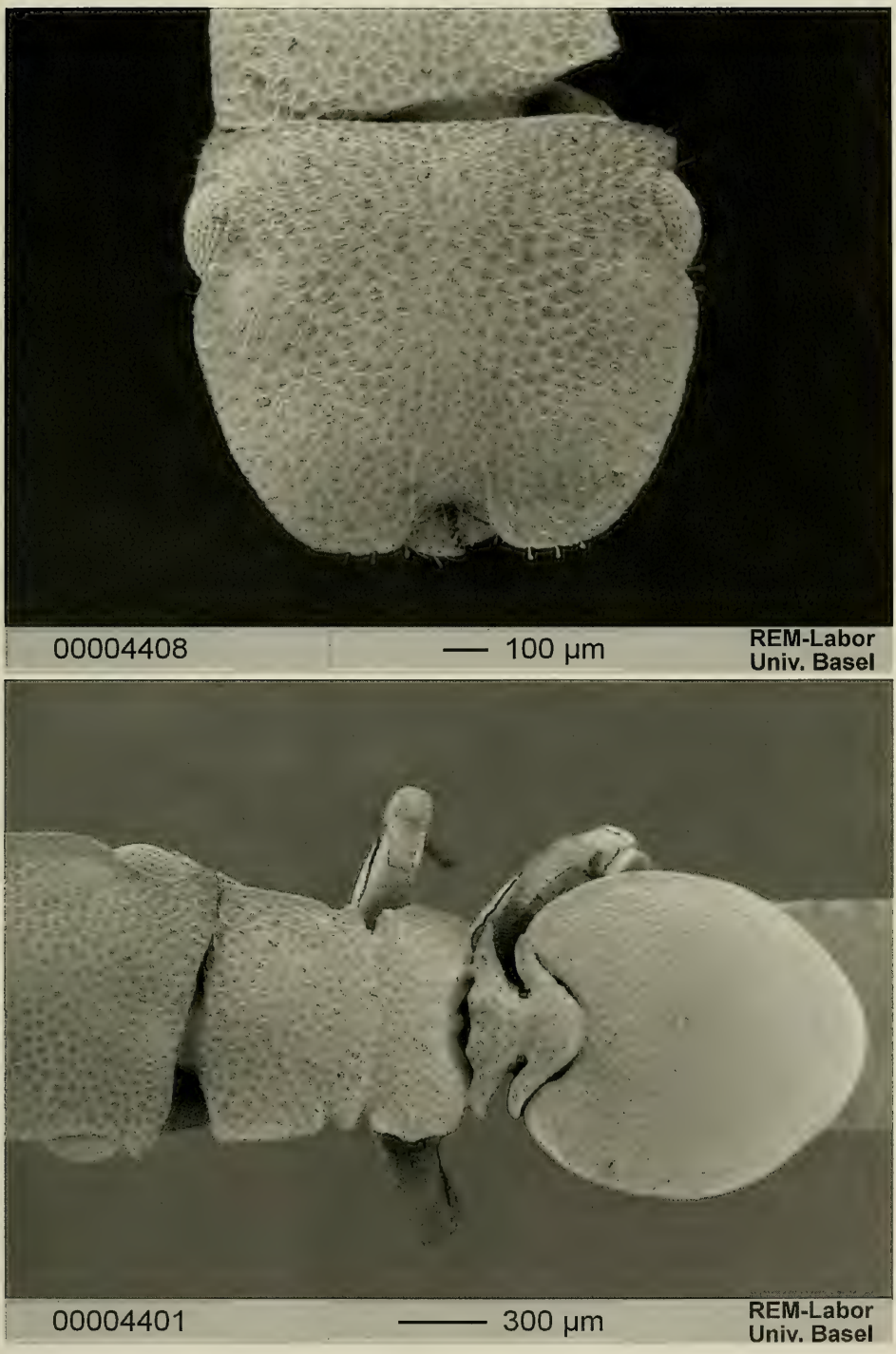


Fig. 222. *Cephalotes pallidoides* DE ANDRADE. Worker from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

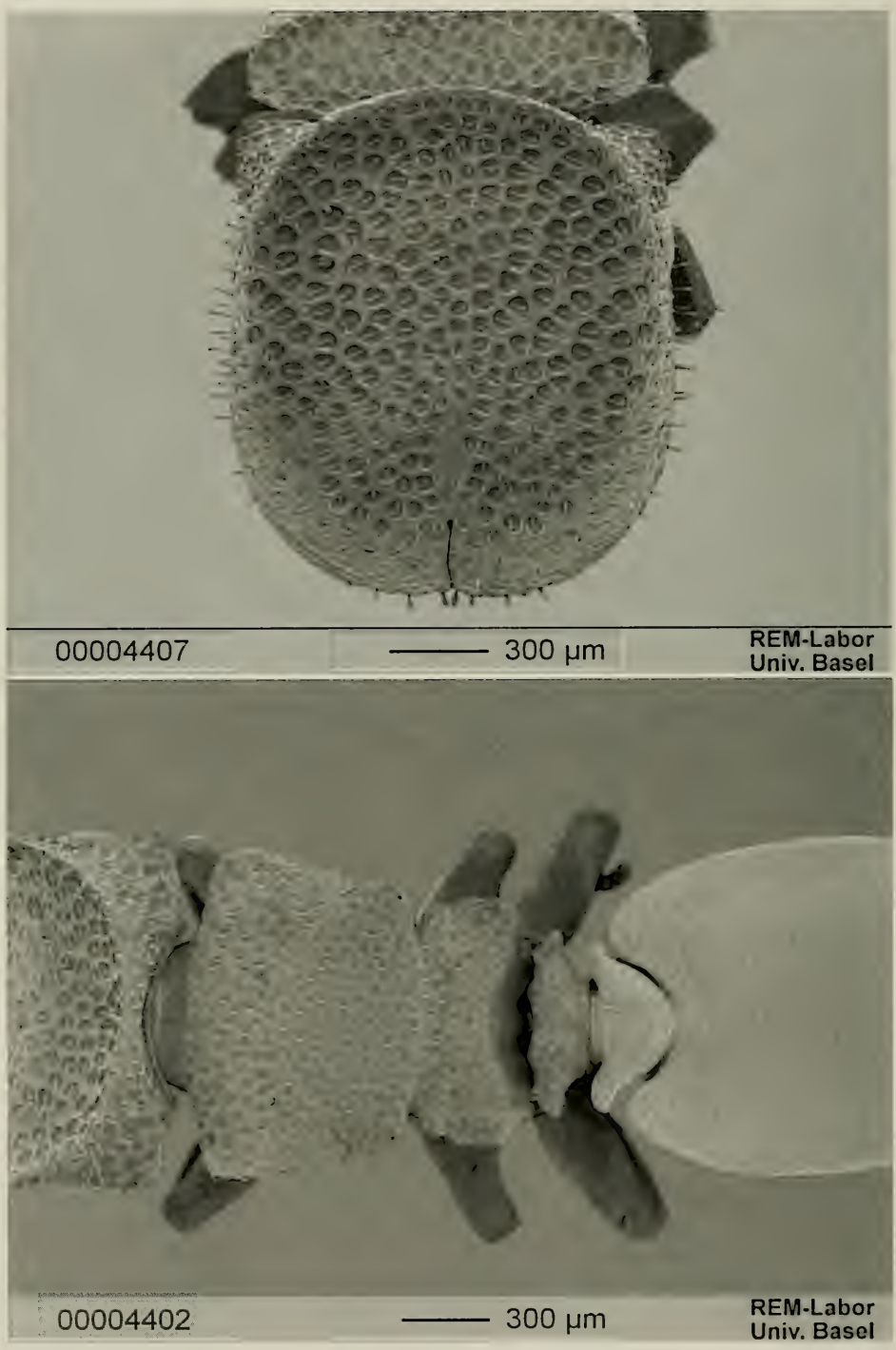


Fig. 223. *Cephalotes pallidoides* DE ANDRADE. Soldier from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

S o l d i e r (Fig. 223). - Differing from *pallidus* in the following characters.

Border of the cephalic disc less crenulate. Disc flat to gently convex medially. Vertexal angles and pronotal carina less crenulate. Sides of the basal face of the propodeum with two pairs of slightly round swellings. Gastral lobes less protruding. Femora more incrassate. Mid and hind femora dorsally more angulate.

Sculpture. Body foveae more regular. Foveae of the head dorsum approaching more the borders of the disc. Internal border of the disc with a narrow punctate area without rugosities. Some specimens with the head completely covered by a thick layer of probable camouflage material. Sides of the head more regularly foveolate. Ventral part of the head with thinner rugosities. Mesosoma, pleurae and pedicel with less impressed punctures and foveae. Gaster and legs with more superficial reticulation, foveae and rugosities.

Pilosity. Sides of the head disc, pronotum, pedicel, gaster and legs with sparser, clubbed hairs. Each fovea of the mesosoma, pedicel, gaster and legs with an appressed hair. Gastral sternites with less, short, erect, pointed, hairs.

Colour. Brown to black.

Measurements (in mm) and indices: TL 5.08–5.64; HL 1.36–1.56; HW 1.22–1.48; EL 0.31–0.34; PW 1.16–1.34; PeW 0.64–0.75; PpW 0.60–0.71; HBaL 0.23–0.25; HBaW 0.13–0.14; CI 89.7–97.4; PI 105.2–114.5; PPeI 181.2–194.2; PPpI 174.6–212.7; HBaI 50.0–61.5.

G y n e . - Differing from the soldier in the following characters. Floor of the disc flat posteriorly, declivous and with raised border anteriorly. Vertexal depression deeper. Humeral angles obtuse. Pronotal carina lower. Pronotum, mesonotum and scutellum flat. Sides of the basal face of the propodeum anteriorly convex and posteriorly with a pair of minute denticles slightly diverging externally.

Anterior face of the petiole more oblique and gently concave medially. Petiolar sides with a pair of small denticles. Postpetiolar sides with a pair of expansions variably developed, round apically or, sometimes, bearing a pair of minute denticles pointed backwards.

Gastral lobes more protruding.

Legs as in the soldier.

Sculpture. As in the soldier but the foveae cover the whole disc. Foveae on the mesosoma variably impressed. Foveae on the propodeum slightly smaller. Upper mesopleurae and center of the lower mesopleurae foveolate, th foveae denser and deeper on the upper mesopleurae.

Pilosity. As in the soldier except for the slightly denser clubbed hairs on the mesosoma, pedicel, gaster, and legs.

Colour. As in the soldier.

Measurements (in mm) and indices: TL 7.22–7.84; HL 1.48–1.64; HW 1.32–1.52; EL 0.36–0.39; PW 1.32–1.48; PeW 0.52–0.66; PpW 0.62–0.74; HBaL 0.32–0.37; HBaW 0.18–0.20; CI 89.2–92.7; PI 100.0–109.1; PPeI 212.9–253.8; PPpI 180.1–212.9; HBaI 50.0–59.4.

M a l e . - Differing from *pallidus* in the following characters.

Frontal carinae lower. Clypeus convex posteriorly, straight or with a superficial incision anteriorly. Pronotum in dorsal view with the sides diverging backwards; lateral margination of the pronotum variably developed.

Genitalia and subgenital plate as in Fig. 224.

Sculpture. Head dorsum minutely reticulate; posterior third of the head dorsum irregularly foveolate-rugose; frons with sparse, small foveae and thin, longitudinal rugosities. Sides of the head in front of the eyes and area between the scapes with thin, transversal rugosities. Ventral part of the head, mesosoma and pedicel as in *pallidus* except for the presence of longitudinal rugosities on the declivous face of the propodeum; rugosities on the mesopleurae more impressed. Gaster subopaque to shining.

Pilosity as for the other species of the group.

Colour. Black with lighter pedicel and gaster. Coxae and two proximal thirds of the femora brown. Remaining parts of the legs dark yellow.

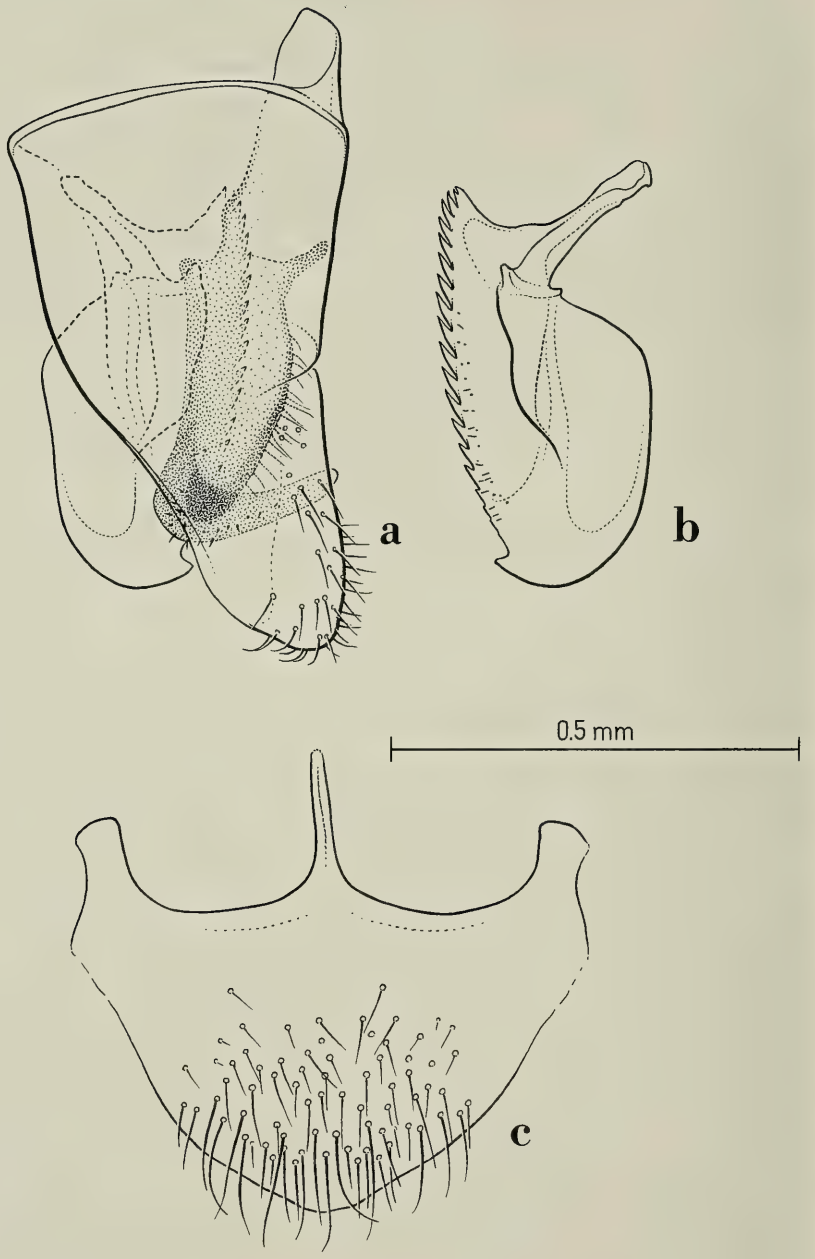


Fig. 224. *Cephalotes pallidoides* DE ANDRADE. Male from Lins (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Measurements (in mm) and indices: TL 4.46–5.17; HL 0.71–0.75; HW 0.88–0.96; EL 0.35–0.40; PW 0.88; PeW 0.39; PpW 0.43–0.47; HBaL 0.39–0.46; HBaW 0.07–0.08; CI 123.9–128.0; PI 100.0–109.1; PPeI 225.6; PPpI 187.2–204.6; HBaI 17.4–17.9.

Material examined. - **Venezuela**: Aragua: El Limon, 450 m, 23.V.1979, 1 gyne, F. FERNÁNDES [MCZC]. Monagas: Barrancas, R. Orinoco, Jan. - Feb. 1935, 3 workers, N. A. WEBER [MCZC].

Trinidad & Tobago: Trinidad: St. Augustine, 28.XI.1934, 2 workers, 1 gyne, N. A. WEBER [MCZC]; same locality, 9 & 18.V.1935, 2 workers, 1 male, N. A. WEBER [MCZC]; same locality, 22.V.1936, 1 gyne, N. A. WEBER [MCZC]; same locality, 1 worker, N. A. WEBER [MCZC]; Arena Forest Reserve, S of Arima, 12.XII.1934, 1 worker, N. A. WEBER [MCZC].

Guyana: Forest Settlement, 22.VIII.1935, 1 gyne, N. A. WEBER [MCZC].

Brazil: Amazonas: Coary, 1 gyne, V. DE ARAÚJO [MZSP]; Ilha de Curari, várzea, 12.II.1976, 2 workers, 1 soldier, J. ADIS [INPA]; Res. Fl. A. Ducke, 16.III, 15.VII, 15 & 27.X, 29.XI.1982, 21.VIII.1991, 23.II & 26.VIII.1992, 9 workers, 2 soldiers, A. ADIS et al. [INPA]; Rio Solimões, Ilha de Marchantaria, 59°58' W, 3°15' S, Lago Camaleão, várzea, 02.IX.1992, 1 worker, ADIS et al. [INPA]. Pará: Conceição do Araguaia, Serra Embratel, 24.I.1983, 3 workers, A. Y. HARADA [INPA]; Serra Norte, Canga, 17–20.VI.1986, 1 gyne [MPEG]; Tocantins Itaguatins, 17–19.VII.1989, 1 worker, F. F. RAMOS [MPEG]. Mato Grosso: Vila Vera, X.1973, 3 workers, 2 gynes, M. ALVARENGA [MZSP]; Barra do Tapirapé, 05.XII.1960, 3 workers, 1 gyne, B. MALKIN [MZSP]; Utiariti (325 m), Rio Papagaio, VII.1961, 8 workers, 1 soldier, 1 male (type series), K. LENKO [MZSP]. Goiás: Jataí, XII.1972, 1 soldier, F. M. OLIVEIRA [MZSP]. São Paulo: Lins, Sept. 1995, 4 workers, 1 soldier, 2 males, M. L. DE ANDRADE [MCZC, NHMB]; Magda, Rio Preto, 01–10.I.1959, 1 gyne, J. LANE [MZSP].

Bolivia: Río Guapay, 1 worker, LIZER & DELÉTANG [NHMB]; Espia, Río Bopi, 2 workers, 1921–22, W. M. MANN [MZSP].

Discussion. - *C. pallidoides* is similar to *pallidus* but the differences in morphology and sculpture listed above proved to be consistent among all the specimens of the two species we examined.

The variability we observed affects essentially the following characters:

1. Most workers from S. Paulo and Mato Grosso (Vila Vera) differ from those from Amazonas (except one from Solimões) by the much narrower head and by the hairs on the border of the frontal carinae sparser.

2. Workers and soldiers from Amazonas (except one from Solimões) have larger PPpI.

3. Camouflage material on the soldier disc has been observed only in specimens from Amazonas.

4. Part of the gynes from Southern Brazil (Magda and Barra do Tapirapé) differ from the others by the smaller and less contiguous foveae on the head dorsum.

5. The hind basitarsi of the gyne from Barra do Tapirapé (those of the Magda specimen are missing) are narrower than among the other gynes examined.

There is, hence, a possibility that the material from SW Brazil may prove to be heterospecific with true *pallidoides*. A decision in this sense is not possible on the material available.

This species has been described largely on material already examined by KEMPF (1958 a) and confused with *pallens*. The misidentification of the record of *varians* by WEBER (1938) from Trinidad is deduced from the fact that *pallidoides* seems to be the sole species of the clade present on the island.

Distribution: Venezuela, Trinidad, Guyana, Brazil, Bolivia.

Cephalotes porrasi (WHEELER) new combination
Figs. 225, 226, 227, 228, 229, 391

Cryptocerus pallens var. *porrasi* WHEELER, 1942: 210, pl. 52, figs. a, b (soldier), c (worker). Worker, soldier, gyne and male. Original description. Type locality: Quebrada de Oro (Canal Zone, Panama). Type material: 8 workers, 4 soldiers labelled: "Quebrada de Oro, C. Z., Mar. 13.1943, W. M. W, *Cordia alliodora*, cotype 1–12, 21093–21094", MCZC.

Paracryptocerus pallens (KLUG), KEMPF, 1958 a: 151 (partim). Misidentification.

Zacryptocerus pallens porrasi, WHEELER & HÖLLDOBLER, 1985: 338, figs. 7–9. Soldier. First combination in *Zacryptocerus*.

Zacryptocerus porrasi (WHEELER), HESPENHEIDE, 1986: 395.

D i a g n o s i s . - A member of the *pallens* clade characterised by the following apomorphies: worker with the membranaceous expansions of the propodeum with two or three teeth, with the hind femora narrowly crested or carinate and with HBaI $\leq$ 34, soldier and gyne with thick, brush-shaped hairs on the head.

W o r k e r (Fig. 225). - Similar to the other species of the group from which it differs for one or more of the following characters. Head broader than long. Frontal carinae with minutely crenulate border. Membranaceous expansions of the vertexal angles narrow. Pronotum with a pair of membranaceous expansions continuous or superficially incised. Mesonotum with a pair of triangular, semi-membranaceous teeth and, in some specimens, an additional pair of minute denticles. Propodeal sides with a pair of membranaceous expansions bi- or tri-toothed. Anterior border of the petiole with a pair of salient swellings. Petiolar sides with a pair of pointed spines as long as or slightly shorter than their maximum length. Postpetiolar sides with a pair of pointed spines directed forwards. Gaster suboval and with a pair of anterolateral membranaceous expansions surpassing the stigma posteriorly and continuing until the posterior border of the first tergite as a superficial margin. Hind and mid femora angulate; their distal part with a dorsal, longitudinal carina less impressed on the mid femora; few specimens with a narrow crest on the hind femora.

Sculpture. Head dorsum and mesosoma minutely punctate, reticulate and with superficial, dense foveae, smaller behind the clypeus, sparser, shallower and less regular on the frontal carinae. Frontal carinae with additional, oblique, thin rugosities. Ventral part of the head reticulate; some specimens with small, dense, irregular foveae and rugosities on the anterior half. Pedicel minutely reticulate-punctate and with small, slightly irregular foveae. Pleurae strongly reticulate and with few, thin, longitudinal rugosities. Anterior third of the first gastral tergite strongly reticulate and with superficial, irregular foveae separate by thin, slightly longitudinal rugosities; similar sculpture on the remaining parts of the tergite but less impressed. Gastral sternites strongly reticulate, the reticulation more superficial on the center of the first sternite. Legs strongly reticulate and with minute, superficial, foveae, more impressed and denser on the outer face of the tibiae.

Pilosity. Body foveae with appressed hairs. Vertexal angles, posterior border of the gastral tergites and legs with rare, clubbed hairs. Gastral sternites with two types of pointed hairs: (1) sparse and short, and (2) rare and long on the second gastral sternite only. Remaining body parts without foveae with sparse, appressed, thin, short hairs only.

Colour. Brown to black with the frontal carinae and the membranaceous expansions of the body slightly lighter.

Measurements (in mm) and indices: TL 3.44–4.34; HL 0.84–1.02; HW 0.96–1.14; EL 0.22–0.24; PW 0.73–0.95; PeW 0.60–0.76; PpW 0.55–0.67; HBaL 0.29–0.36; HBaW 0.10–0.12; CI 112.0–116.3; PI 120.0–131.5; PPeI 121.7–137.3; PPpI 132.7–148.4; HBaI 31.4–34.0.

S o l d i e r . - Head disc suboval, longer than broad. Border of the disc strongly raised and with crenulate margin posteriorly. Floor of the disc medially with a pointed tumulus. Posterior part of the disc depressed.

Mesosoma. Humeral angles with a pair of obtuse, semi-membranaceous teeth. Pronotal sides gently converging posteriorly. Pronotal carina well marked, with variably crenulate

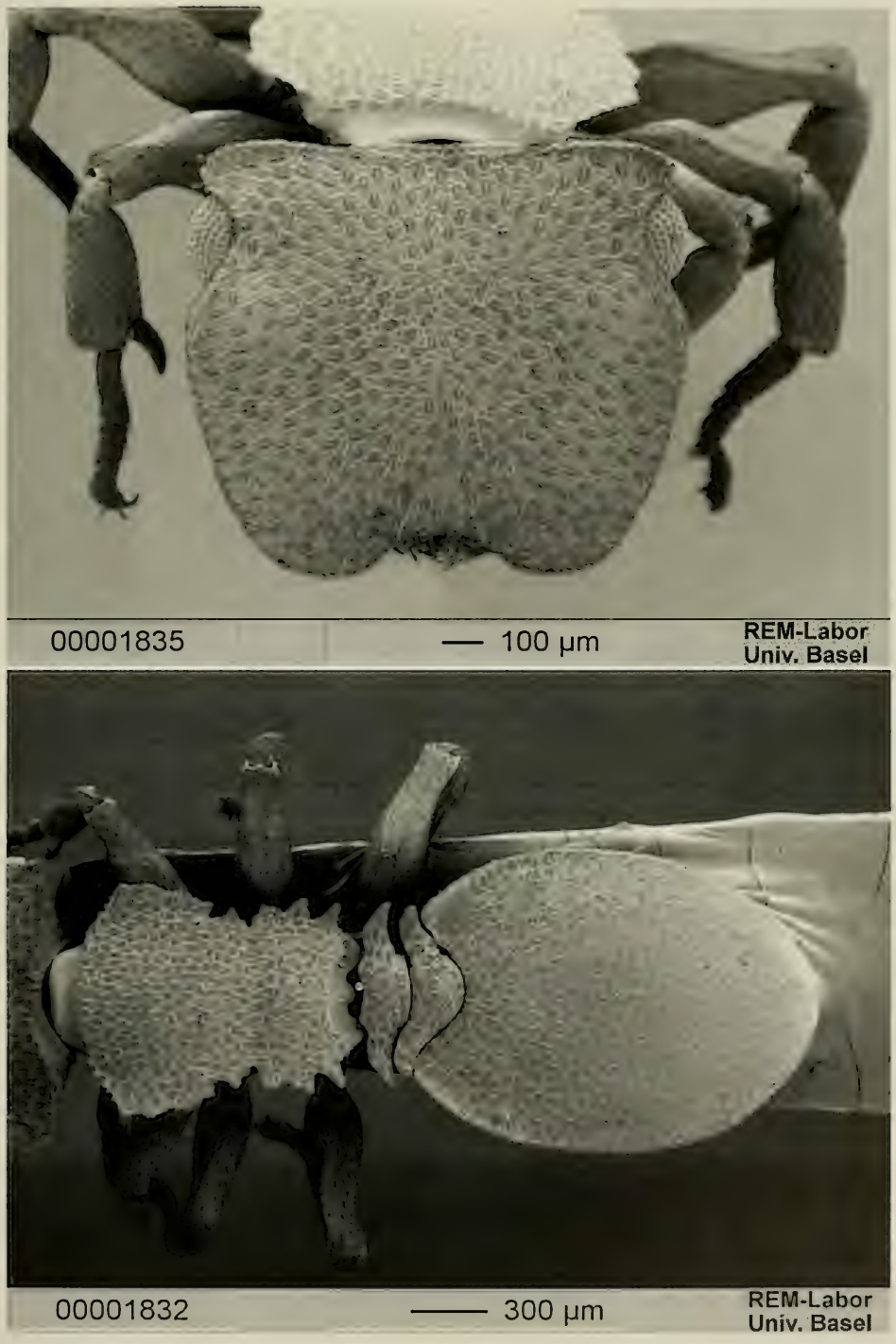


Fig. 225. *Cephalotes porrasi* (WHEELER). Worker from Paraiso, Panama Canal Zone: head (top) and meso- and metasoma (bottom) in dorsal view.

margin and shortly interrupted medially. Mesonotal sides with a pair of broad, triangular teeth, sometimes with almost round tip. Propodeum with differentiate basal and declivous faces; sides of the basal face gently convex or with a small pair of irregular teeth followed by a pair of short, stout teeth curved upwards in large specimens.

Pedicel as in the worker but with narrower and shorter spines.

Mid and hind femora dorsally angulate; hind femora superficially carinate dorsally.

Gaster oval and with a pair of protruding lobes with marked margins.

Sculpture. Head dorsum with large, deep foveae, smaller on the tumulus, denser almost on the whole disc in small specimens and more clumped on the two posterior thirds of the floor of the disc than on its borders of the larger soldiers. Interspaces between the foveae porous. Sides of the disc punctate, densely and irregularly foveolate-rugulose, the foveae diminishing in size anteriorly; in some specimens the foveae more regular around the eyes; in other specimens the sides of the disc completely covered by slightly longitudinal rugosities. Ventral part of the head punctate, variably shining and covered by small foveae and irregular rugosities less impressed on median part. Mesosoma minutely reticulate-punctate and with dense foveae, larger on the pronotum, smaller on the propodeum. Pedicel with sculpture similar to that on the propodeum but with smaller foveae. Pleurae strongly reticulate; propleurae variably and irregularly foveolate-rugose. Gaster and legs with sculpture similar to that of the worker.

Pilosity. The foveae on the head dorsum with an erect, brush-shaped hair of variable size; those on the mesosoma, pedicel, gaster and legs with an appressed or decumbent, weakly canaliculate hair. Borders of the disc and foveae of the sides of the head with erect, long, variably clavate hairs; some specimens with rare brush hairs originating from the lateral foveae. Vertexal angles, pronotum, pedicel, gastral tergites and legs with rare clubbed hairs. Gastral sternites with two types of pointed hairs: sparse and short, and rare and long on the second gastral sternite only. Body parts without foveae with sparse, appressed, thin, short hairs.

Colour. Dark brown to black.

Measurements (in mm) and indices: TL 5.52–7.12; HL 1.52–1.92; HW 1.44–1.72; EL 0.29–0.32; PW 1.32–1.68; PeW 0.76–0.80; PpW 0.69–0.80; HBaL 0.37–0.40; HBaW 0.14–0.15; CI 89.6–94.7; PI 102.4–109.1; PPeI 173.7–210.0; PPpI 191.3–210.0; HBaI 37.5–37.8.

G y n e (Figs. 226, 391). - Differing from the soldier in the following details.

Sides of the disc with the borders slightly lower; few specimens with the border very low. Humeral angles with a pair of short, triangular teeth or simply obtuse. Pronotal crest lower. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly convex and posteriorly with a small pair of pointed teeth, slightly diverging laterally or directed backwards in some specimens only.

Petiole. Anterior face oblique and slightly concave. Petiolar sides with a pair of pointed denticles. Postpetiole convex dorsally and with broad lateral spines with truncate apex and pointed backwards.

Gaster. Similar to the one of the soldier but much longer.

Wings as in Fig. 227.

Legs with less impressed carinae on the outer face of the hind femora.

Sculpture. Foveae of the head dorsum slightly larger than in the soldier. Mesonotal foveae shallower. Pleurae reticulate. Propleurae with thin, superficial, slightly longitudinal rugosities. Lower meso- and metapleurae with thin, longitudinal rugosities. Upper mesopleurae and upper border of the upper metapleurae with small foveae.

Pilosity. As in the soldier except for the clubbed hairs thinner, longer and more abundant on the pedicel, on the gaster and on the legs and also present on the whole mesosoma.

Colour. Dark brown to black.

Measurements (in mm) and indices: TL 7.40–8.20; HL 1.52–1.72; HW 1.44–1.56; EL 0.34–0.36; PW 1.28–1.44; PeW 0.64–0.68; PpW 0.77–0.80; HBaL 0.47–0.50; HBaW 0.15–0.16; CI 90.7–94.7; PI 108.3–112.5; PPeI 200.0–211.8; PPpI 166.2–180.0; HBaI 31.9–32.0.

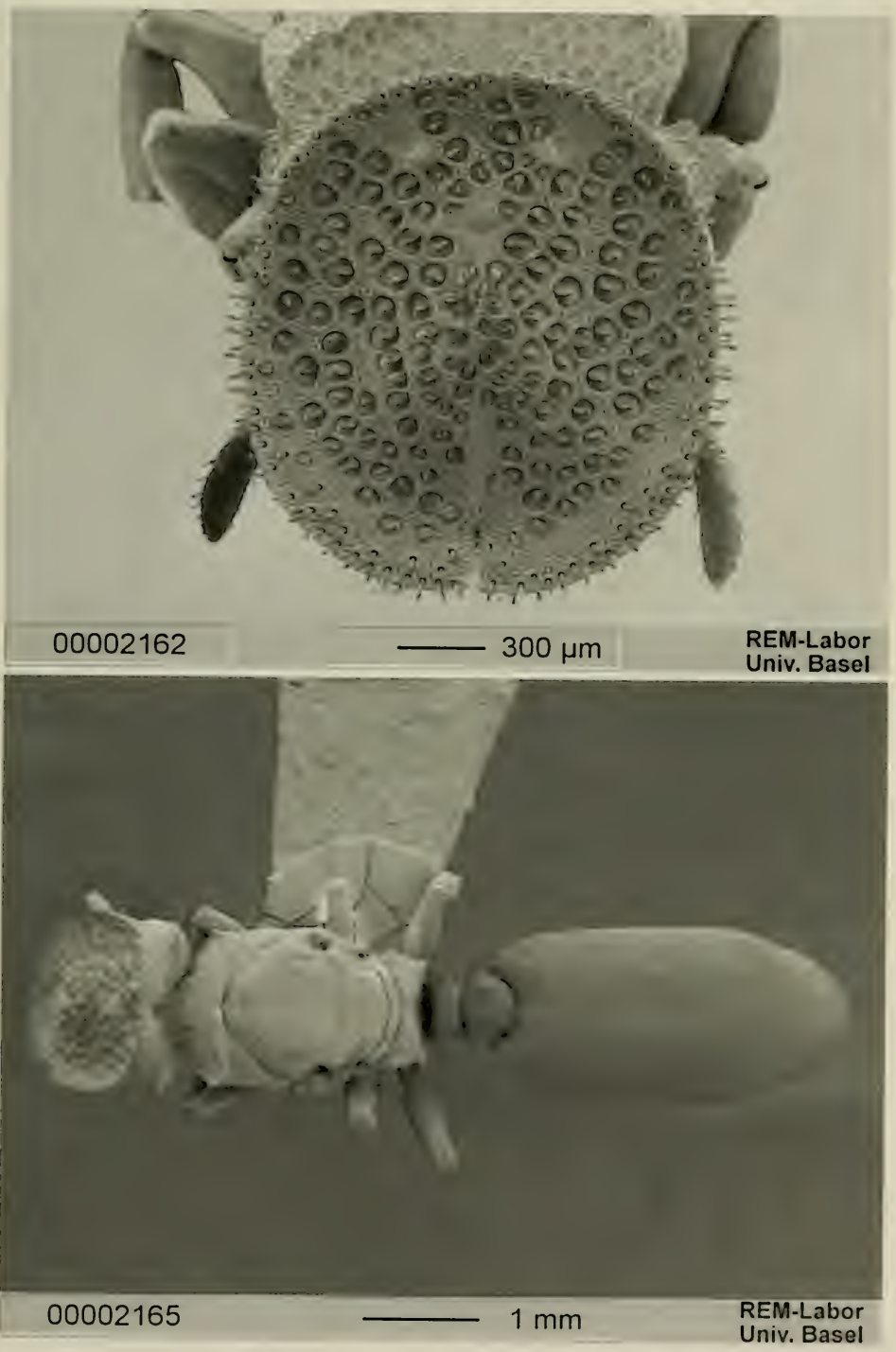


Fig. 226. *Cephalotes porrasi* (WHEELER). Gyne from Frijoles, Panama Canal Zone: head (top) and meso- and metasoma (bottom) in dorsal view.

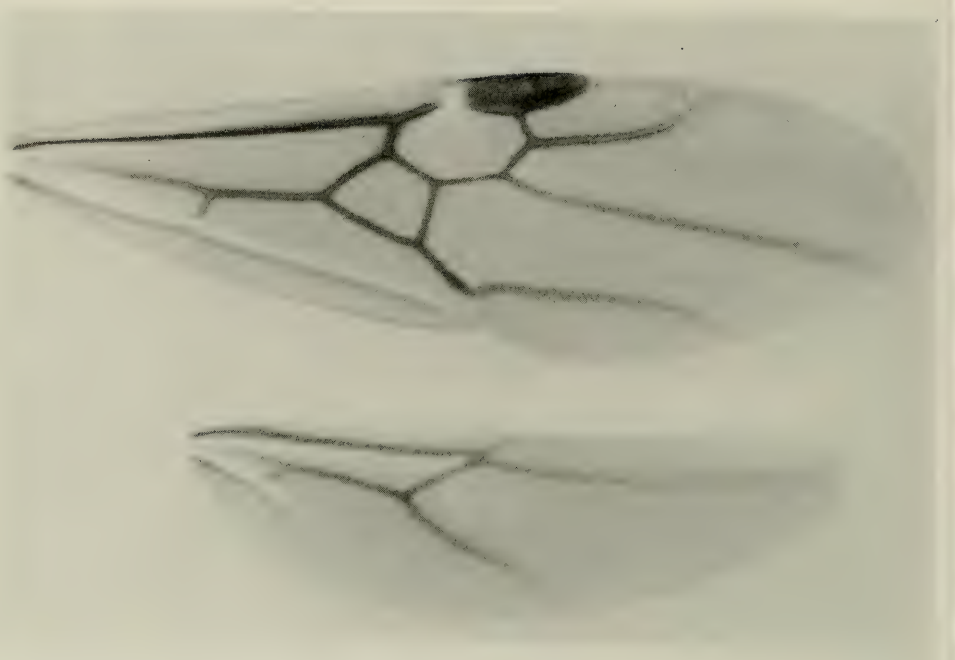


Fig. 227. *Cephalotes porrasi* (WHEELER). Gyne from Frijoles, Panama Canal Zone, fore and hind wings.

M a l e (Fig. 228). - Similar to the other species of the group from which it differs for one or more of the following characters: frontal carinae not raised. Clypeus convex posteriorly and superficially incised anteriorly in some specimens only.

Mesosoma. Pronotum in dorsal view with traces of scapular angles.

Genitalia and subgenital plate as in Fig. 229.

Sculpture. Head dorsum minutely reticulate. Posterior third of the head dorsum irregularly foveolate-rugose; frons with rare, minute foveae. Remaining head dorsum with thin rugosities oriented transversally in front of the eyes and longitudinal on the frons. Ventral part of the head reticulate, irregularly foveolate-rugulose, the rugae oblique to transversal around the eyes. Pronotum minutely reticulate and with irregular foveae, deeper on the sides. Mesonotum with minute, superficial reticulation, variably shining and with small, variably clumped, superficial, foveae. Scutellum with similar sculpture as on the mesonotum but with denser foveae; some specimens with few thin, longitudinal rugosities. Basal face of the propodeum reticulate and longitudinally rugulose. Pedicel with superficial and minute reticulation and with few, small foveae and short rugosities on the sides. Propleurae reticulate and sometimes with few, longitudinal, thin rugosities. Mesopleurae superficially reticulate and with thin, longitudinal rugosities on the posterior half; this sculpture covered by superficial, small foveae on the center of the lower and of the upper mesopleurae. Metapleurae reticulate and irregularly rugose; the rugosities oriented longitudinally on the lower part. Gaster almost smooth and shining. Legs punctate with moderately shining femora.

Pilosity as for the other species of the group.

Colour. Black. Coxae and gaster brown. Legs dark yellow.

Measurements (in mm) and indices: TL 4.82–4.96; HL 0.73–0.75; HW 0.91–0.93; EL 0.35–0.36; PW 0.75–0.80; PeW 0.33–0.34; PpW 0.36–0.39; HBaL 0.54–0.56; HBaW 0.07; CI 124.0–124.6; PI 113.7–124.0; PPeI 220.6–242.4; PPpI 192.3–222.2; HBaI 12.9–12.5.

M a t e r i a l e x a m i n e d . - **Mexico**: V e r a C r u z : Pueblo Nuevo nr. Tetzonapa, 07.VIII.1953, 11 workers, 5 soldiers, E. O. WILSON [MCZC, MZSP].

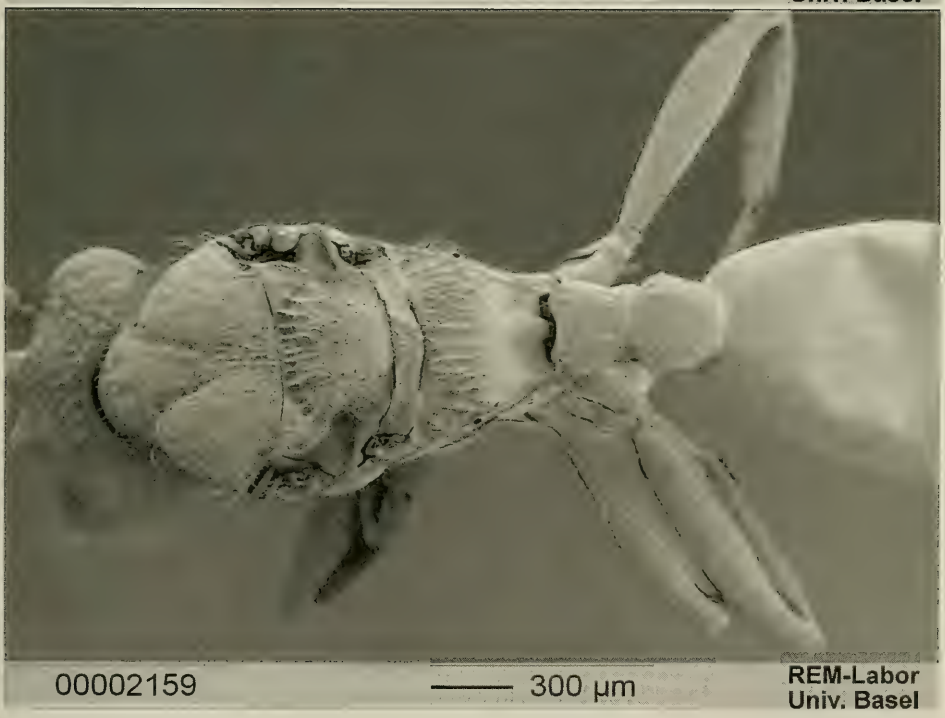


Fig. 228. *Cephalotes porrasi* (WHEELER). Male from Frijoles, Panama Canal Zone: head (top) and meso- and metasoma (bottom) in dorsal view.

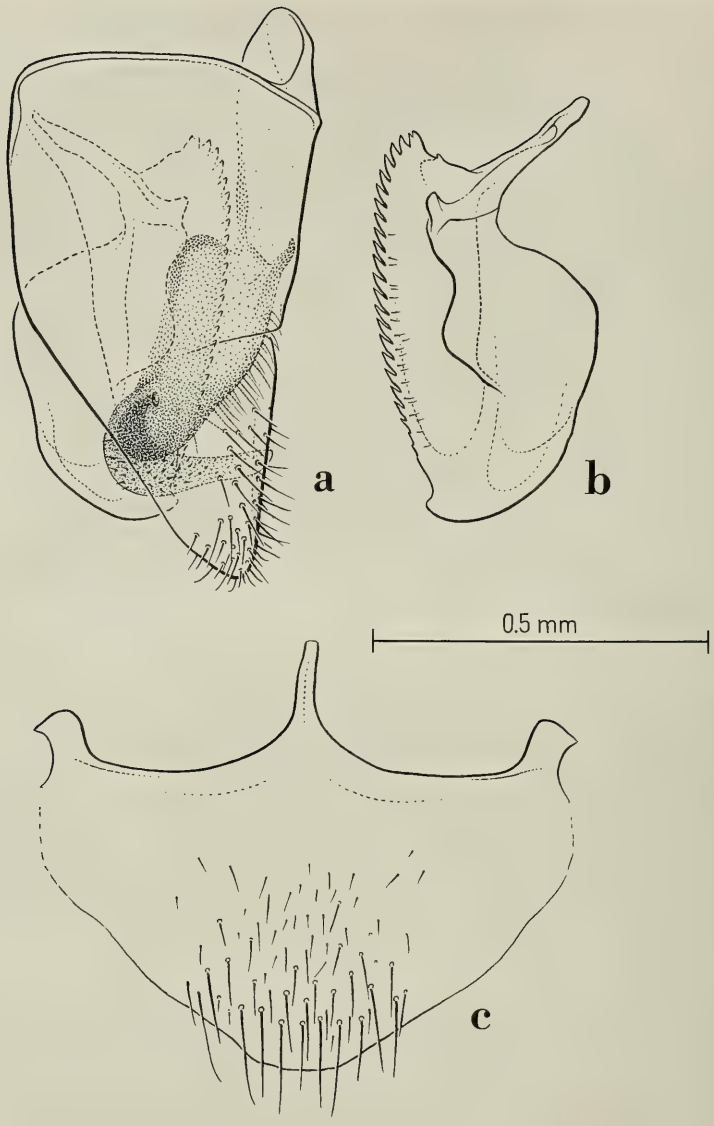


Fig. 229. *Cephalotes porrasi* (WHEELER). Male from Frijoles, Panama Canal Zone. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Belize: El Cayo, VI. 1959, 1 worker, N. L. H. KRAUSS [USNM].

Nicaragua: I. de Diamante, 09–10.X.1994, 2 workers, J. P. CALDWELL [CPCC].

Costa Rica: Sirena, Jul. 1895, 1 worker, [MCSN]; Sirena, Penin. Osa, 82°8' N, 83°35' W, 18.XI.1981, 1 worker, 1 soldier, J. LONGINO [MCZC].

Panama: Quebrada de Oro, Canal Zone, 13.III.1943, in *Cordia alliodora*, 8 workers, 4 soldiers (all syntypes), W. M. WHEELER [MCZC]; Frijoles, Canal Zone, in *Cordia alliodora*, 14 workers, 4 soldiers, 10 gynes, 7 males, WHEELER [MCZC, MZSP]; Red Tank, Canal Zone, in *Cordia alliodora*, 11 workers, 1 soldier, 3 gynes, WHEELER [MCZC, MHNG, MZSP (2 wor-

kers and 1 soldier in MHNG erroneously labelled as syntypes)]; Camaron, Z 686/SK, 27.V.1929, 3 workers, 1 soldier, 1 male, Wm. M. WHEELER [MCZC]; Corozal, Canal Zone, 07.XII.1924, in *Acacia multiglandulosa*, 4 workers, 3 soldiers, W. M. WHEELER [MCZC, MZSP]; Paraiso, Canal Zone, 05.II.1911, 2 workers, E. A. SCHWARZ [USNM]; Summit, Canal Zone, XI.1965, 2 workers, 4 soldiers, 1 gyne, N. L. H. KRAUSS [USNM]; Barro Colorado I., 23.VII.1924, 1 worker, WHEELER [MCZC]; Barro Colorado, Nature Monument, Gigante Peninsula, 18.IV.1992, 5 workers, J. E. TOBIN [MCZC].

Colombia: Antioquia: Río Porce, 1020 m, 1938, 2 workers, N. A. WEBER [MCZC].

Ecuador: Pichincha: 47 km S of Sto. Domingo, Río Palenque, 1975, 1 worker, S. & J. PECK [MCZC].

Discussion. - Synonymised with *pallens* by KEMPF (1958 a), this species reappeared in the literature as a subspecies of *pallens* in WHEELER & HÖLLDOBLER (1985) who give no reasons for it and as a good species in HESPENHEIDE (1986) and LETURNEAU & CHOE (1987) who equally don't justify their action. The latter three authors, however, had their material identified by R. R. SNELLING (personal communication to CBU). The full specific status of *porrasi* has been suggested to us in a personal communication by R. R. SNELLING with whom we entirely agree.

Distribution: Mexico, Belize, Nicaragua, Costa Rica, Panama, Colombia, Ecuador.

Cephalotes pallens (KLUG) new combination
Figs. 230, 231, 232, 233, 234

Cryptocerus pallens, KLUG, 1804: 206. Worker. Original description. Type locality: Brazil. Type material: not available for the present study.

Cryptocerus discocephalus SMITH, 1854: 222, pl. 20, fig. 2. Soldier. Original description. Type locality: Villa Nova (Brazil). Type material presumably lost, neither in BMNH nor in OXUM. Synonymy by EMERY, 1894 a: 212.

Cryptocerus araneolus SMITH, 1854: 223, pl. 19, fig. 4. Worker. Original description. Type locality: Antille St. Vincent. Type material: holotype worker labelled "St. Vincts" in the BMNH, examined. Synonymy by EMERY, 1894 a: 212.

Cryptocerus discocephalus SMITH, SMITH, 1858: pl. 11, figs. 1-3. Worker, soldier and male. Figures only.

Cryptocerus pallens KLUG, EMERY, 1894 a: 212, pl. 4, figs. 29–32. Worker, soldier and gyne.

Paracryptocerus pallens (KLUG), KEMPF, 1958 a: 150. Partim (synonymy and description in part only); nec pl. 8, figs. 5 and 6 = *pallidoides* (q. v.). First combination in *Paracryptocerus*.

Paracryptocerus pallens (KLUG), WHEELER & WHEELER, 1973: 79. Larva.

[*Zacryptocerus pallens*, WHEELER & HÖLLDOBLER, 1985: 338. First combination in *Zacryptocerus*. Misidentification. The specimens cited in this paper belong to *pallidus* (q. v.)].

Diagnosis. - A member of the *pallens* clade differing from its sister species, *porrasi*, by the following apomorphies: in the worker propodeal expansions incised posteriorly, hind femora crested and HBaI > 38, in the soldier and gyne, hind femora carinate and head disc with canaliculate hairs.

Worker (Fig. 230). - Similar to the other species of the group from which it differs for one or more of the following characters. Head broader than long. Frontal carinae with weakly crenulate border. Membranaceous expansions of the vertexal angles variably developed. Pronotum with a pair of broad, membranaceous expansions. Mesonotum with a pair of triangular or subrectangular semimembranaceous teeth. Propodeum with a pair of broad, membranaceous expansions, covering and fused with two-three small teeth and with a deep posterior notch posteriorly less incised among large specimens. Anterior border of the petiole with a pair of salient swellings. Petiolar sides with a pair of pointed spines as long as or longer than the petiole. Postpetiolar sides with a pair of pointed spines directed slightly forwards. Gaster suboval and with a pair of anterolateral membranaceous expansions

surpassing the stigma posteriorly and continuing up to the posterior border of the first tergite as a superficial margin. Hind and mid femora angulate; mid femora dorsally carinate; hind femora dorsally with a developed longitudinal crest.

Sculpture. Head dorsum and mesosoma minutely reticulate-punctate, with dense foveae, smaller on and behind the clypeus, sparser, shallower and irregular on the frontal carinae. Frontal carinae with additional, oblique, thin rugosities. Ventral part of the head reticulate; some specimens with longitudinal rugosities on the two anterior thirds. Pedicel minutely reticulate-punctate and with small, irregular foveae. Pleurae strongly reticulate and with few, thin, longitudinal rugosities; in some specimens the rugosities denser and more impressed. First gastral tergite reticulate; its sides with superficial, irregular foveae separate by few, thin, irregular, longitudinal rugosities extending to the anterior third in some specimens. Remaining gastral tergites and sternites simply reticulate, with the sides of the first gastral sternite superficially foveolate-rugulose in some specimens only; center of the first gastral sternite with less impressed reticulation and superficially shining. Legs strongly reticulate and with minute, superficial, irregular foveae, more impressed and denser on the outer face of the tibiae.

Pilosity. Body foveae with appressed hairs. Posterior part of the frontal carinae in front of the eyes, vertexal angles, posterior border of the gastral tergites, and legs with rare, clubbed hairs. Gastral sternites with two types of pointed hairs: (1) sparse and short, and (2) rare and long on the second gastral sternite only. Body parts without foveae with sparse, appressed, thin, short hairs.

Colour. Brown to black with the frontal carinae and the membranaceous expansions of the body slightly lighter.

Measurements (in mm) and indices: TL 3.73–5.38; HL 0.88–1.16; HW 0.98–1.40; EL 0.20–0.30; PW 0.84–1.22; PeW 0.64–0.83; PpW 0.54–0.81; HBaL 0.24–0.34; HBaW 0.10–0.13; CI 108.9–120.7; PI 111.4–117.8; PPeI 115.7–162.7; PPpI 143.3–166.7; HBaI 38.2–45.8.

S o l d i e r (Fig. 231). - Head disc suboval, longer than broad. Border of the disc strongly raised and with superficially crenulate margin posteriorly, the crenulation stronger in small specimens. Floor of the disc medially with a gently convex tumulus. Posterior part of the disc variably depressed.

Mesosoma. Humeral angles with a pair of obtuse, semi-membranaceous teeth. Pronotal sides straight or gently converging posteriorly. Pronotal carina well marked, with variably crenulate margin and shortly interrupted medially. Mesonotal sides with a pair of broad, triangular or round teeth. Propodeum with differentiate basal and declivous faces; basal face almost as broad as the mesonotum; sides of the basal face convex or diverging backwards into a small pair of irregular teeth followed by a pair of short, stout teeth curved upwards in large specimens.

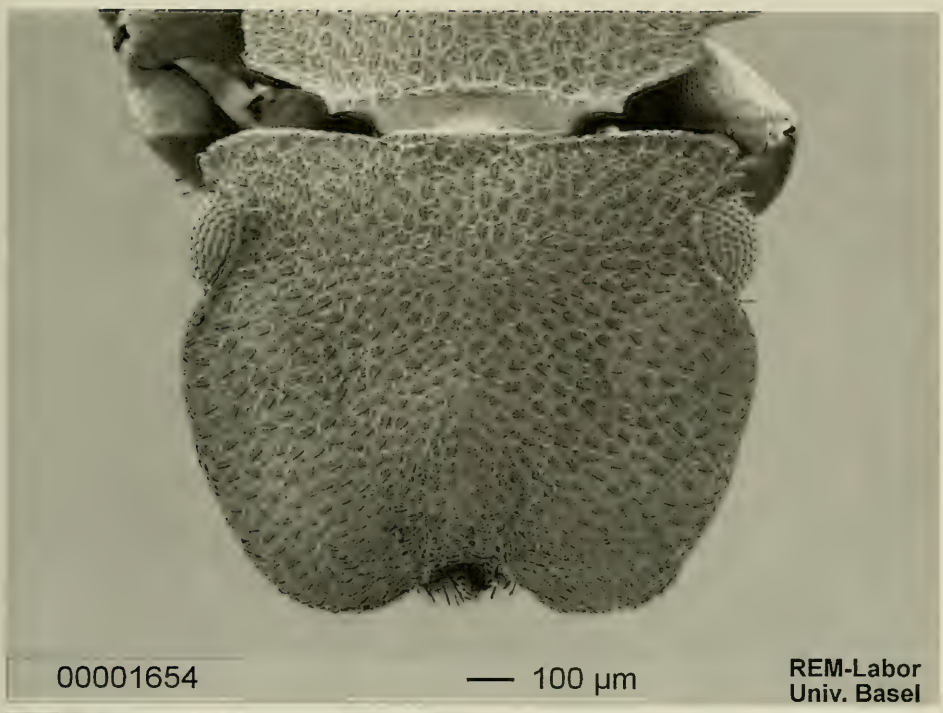
Pedicel as in the worker but with narrower and shorter spines.

Mid and hind femora angulate; hind femora carinate.

Gaster oval and with a pair of protruding anterior lobes with marked margins.

Sculpture. Head dorsum with sparse and shallow foveae, the fovea rare on the anterior half, rarely denser and deeper on the whole disc; this morphology is more frequent among small specimens. Interspaces between the foveae porous. Sides of the disc densely and irregularly foveolate-rugulose, the foveae diminishing in size anteriorly, sometimes with superimposed longitudinal rugosities. Ventral part of the head punctate, variably shining and covered by small foveae and irregular rugosities superficial in the center, more longitudinal postero-laterally and more transversal anterolaterally. Mesosoma minutely reticulate-punctate and with dense foveae less regular and shallower on the middle of the mesonotum and on the basal face of the propodeum of some specimens, larger on the pronotum, smaller on the propodeum. Pedicel minutely reticulate-punctate and with small, irregular foveae. Pleurae strongly reticulate; propleurae variably foveolate-rugose, the rugae oblique to transversal. Lower parts of the meso- and of the metapleurae with longitudinal rugosities and small foveae; some specimens either simply rugose or foveolate only. Gaster and legs with sculpture similar to that of the worker.

Pilosity. The foveae on the head dorsum with a subdecumbent to appressed, canaliculate hair; those on the mesosoma, pedicel, gaster and legs with an appressed one. Borders of the



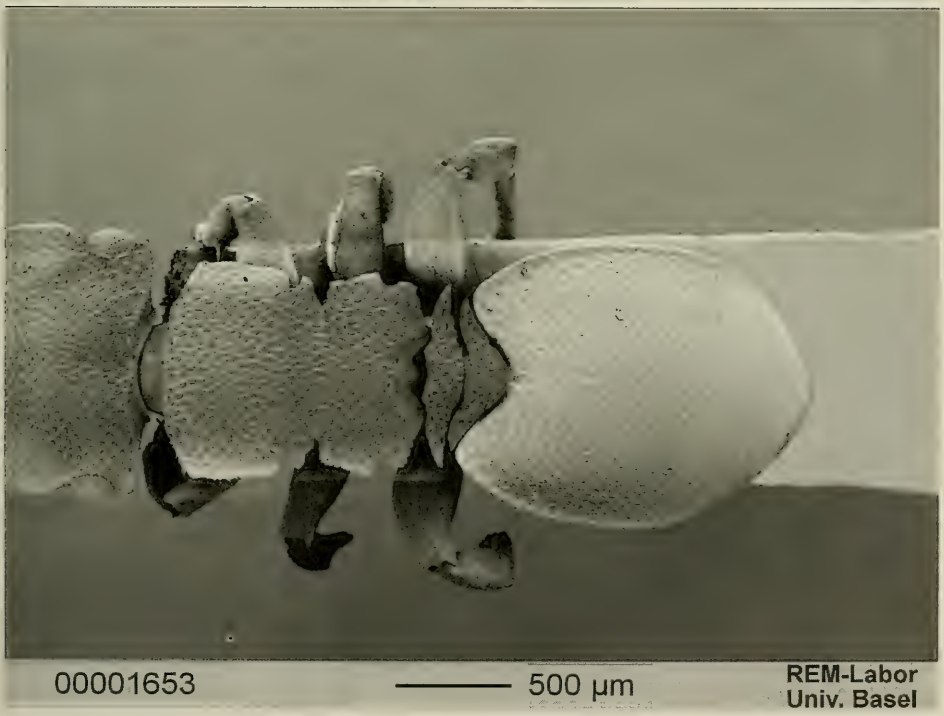


Fig. 230. *Cephalotes pallens* (KLUG). Worker from Nariva Swamp, Trinidad: head (top) and meso- and metasoma (bottom) in dorsal view.

disc and foveae on the sides of the head with erect, long, variably clavate hairs. Vertexal angles, pronotum, pedicel, first gastral tergite, posterior borders of the remaining tergites and sternites and legs with rare, clubbed hairs. Gastral sternites, in addition, with two types of pointed hairs: (1) sparse and short, and (2) rare and long on the second and on the third gastral sternites. Body parts without foveae with sparse, appressed, thin, short hairs.

Colour. Dark brown to black.

Measurements (in mm) and indices: TL 5.16–7.72; HL 1.36–1.96; HW 1.28–2.00; EL 0.27–0.36; PW 1.22–1.84; PeW 0.61–0.89; PpW 0.57–0.83; HBaL 0.24–0.36; HBaW 0.12–0.15; CI 89.5–94.1; PI 101.2–108.7; PPeI 187.7–217.9; PPpI 213.3–221.7; HBaI 40.6–50.0.

G y n e (Fig. 232). - Differing from the soldier in the following details.

Sides of the disc with less raised borders. Posterior border of the disc much more crenulate. Maximum disc concavity usually anterior. Humeral angles with a pair of small, triangular teeth or simply obtuse. Pronotal carina lower. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly convex or triangular and posteriorly with a small pair of pointed teeth, slightly diverging laterally.

Petiole with oblique anterior face; its sides with a small pair of denticles. Postpetiole convex dorsally and with a pair of round or pointed teeth pointed backwards.

Gaster. Similar to the one of the soldier but much longer and with more protruding lobes.

Legs with less salient carinae of the mid and hind femora.

Wings as in Fig. 233.

Sculpture. Foveae of the head dorsum denser, larger and deeper than in the soldier. Mesonotal foveae shallower. Propodeal foveae deeper. Pleurae reticulate. Propleurae with foveae on the upper part and with thin, oblique to longitudinal rugosities on the lower part. Upper and center of the lower mesopleurae foveolate, the foveae deeper and denser on the upper part. Metapleurae with longitudinal rugosities on the lower part and with small foveae on the upper border. Occasionally the anterior third of the first gastral tergite with deeper foveae and rugae.

Pilosity. As in the soldier except for the hairs of the disc, suberect to subdecumbent, and for the clubbed hairs more abundant on the pedicel, on the gaster and on the legs and extending to the whole mesosoma.

Colour. Dark brown to black.

Measurements (in mm) and indices: TL 8.00–8.28; HL 1.64–1.76; HW 1.52–1.60; EL 0.38–0.39; PW 1.44–1.56; PeW 0.55–0.65; PpW 0.70–0.77; HBaL 0.40–0.43; HBaW 0.16–0.17; CI 87.5–92.7; PI 102.6–106.9; PPeI 240.0–261.8; PPpI 194.6–205.7; HBaI 37.2–42.5.

M a l e . - Similar to the other species of the group from which it differs for one or more of the following characters. Frontal carinae not raised. Clypeus convex posteriorly and straight anteriorly. Pronotum in dorsal view with traces of scapular angles.

Sculpture. Head dorsum minutely reticulate and irregularly foveolate-rugose on its posterior third. Frons with rare, minute foveae. Remaining dorsal surfaces of the head with thin rugosities, transversal close to the eyes and longitudinal between the ocelli. Ventral part of the head reticulate and with irregular, oblique rugae. Pronotum minutely reticulate and with small, superficial foveae, deeper on the sides. Mesonotum with minute, superficial reticulation and with small, faint, sparse, foveae. Scutellum similarly sculptured and with thin, longitudinal rugosities. Basal face of the propodeum reticulate and with irregular, longitudinal rugosities. Propleurae reticulate, sometimes with few, longitudinal, thin rugosities. Mesopleurae superficially reticulate and with thin, longitudinal rugosities on the posterior half; this sculpture covered by few, superficial, small foveae on the center of the mesopleurae. Metapleurae reticulate and irregularly rugose, the rugosities more longitudinal on the lower part. Pedicel with superficial and minute reticulation and with few, short rugosities on the sides. Gaster superficially reticulate and slightly shining. Legs punctate with moderately shining femora.

Pilosity as for the other species of the group.

Genitalia and subgenital plate as in Fig. 234.

Fig. 231. *Cephalotes pallens* (KLUG). Soldier from Guatemala: head (top) and meso- and metasoma (bottom) in dorsal view.

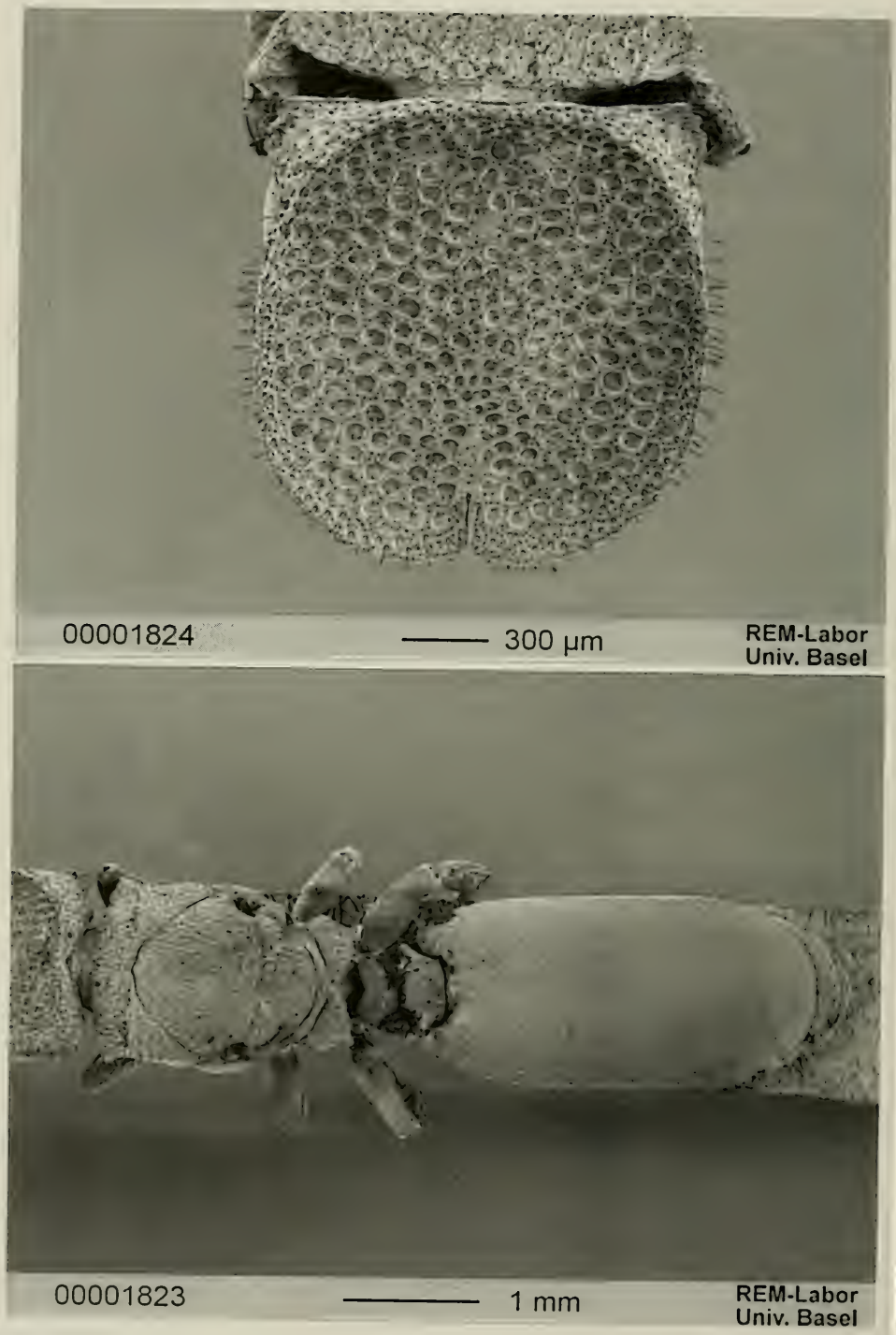


Fig. 232. *Cephalotes pallens* (KLUG). Gyne from Mérida, Venezuela: head (top) and mesoand metasoma (bottom) in dorsal view.

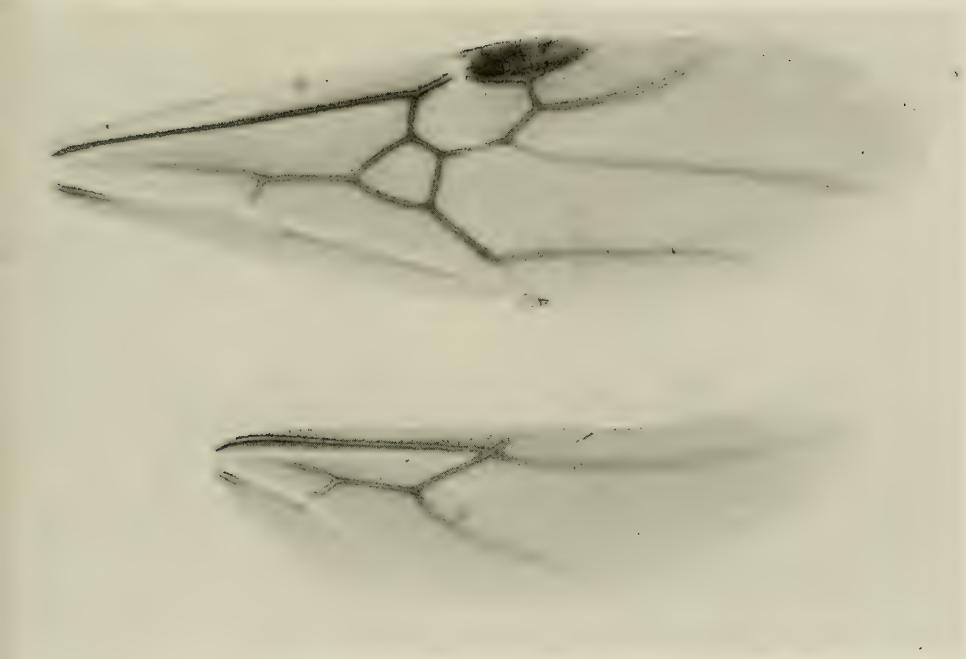


Fig. 233. *Cephalotes pallens* (KLUG). Gyne from Mérida, Venezuela, fore and hind wings.

Colour. Black. Pedicel, coxae and gaster brown. Legs dark yellow with slightly darker tarsomeres.

Measurements (in mm) and indices: TL 4.18–4.47; HL 0.65–0.72; HW 0.85–0.90; EL 0.34–0.39; PW 0.72–0.80; PeW 0.31; PpW 0.36; HBaL 0.43–0.52; HBaW 0.06–0.07; CI 125.0–130.8; PI 112.5–118.0; PPeI 232.2; PPpI 200.0; HBaI 13.2–13.9.

Material examined: **Mexico**: no further locality, 21.II.1939, intercepted in Brownsville, on *Euphorbia*, 5 workers, 1 soldier, 1 gyne [USNM]; no further locality, 8.VIII.1946, intercepted in Brownsville, on *Laelia* sp. 2 workers [MZSP]; no further locality, 03.III.1958, intercepted in Brownsville, on Bromeliads, 8 workers, 8 soldiers, HEINRICH [USNM]. Chiapas: San Sebastian, 14.I.1907, 17 workers, 4 soldiers, G. N. COLLINS [MCZC, USNM]; Tuxtla Gutierrez, VIII.1959, 1 worker, N. L. H. KRAUSS [USNM].

Guatemala: no further locality, 15.I.1940, intercepted in New York, on *Primavera*, 30 workers, 8 soldiers, 2 gynes [MZSP, USNM]; no further locality, 19.III.1946, intercepted in San Francisco, on *Epidendrum*, 3 workers, [MZSP]; Zacapa, 12–21.XII.1911, 3 workers, W. M. WHEELER [MCZC]; Patulul, 07.I.1912, 1 worker, 1 soldier, 1 gyne, WHEELER [MCZC].

Costa Rica: no further locality, 4 workers, 2 soldiers [MHNG]; no further locality, 3 workers, 3 soldiers, 1 gyne, ALFARO [MCSN]; no further locality, 2 workers, 1 soldier, MONTERO [MCSN]; Guanac. Prov., El Coco, 23.VII.1965, 1 worker, 1 soldier, F. COYLE [MZSP]; San José, 1940, 3 workers, 1 gyne, H. SCHMIDT [MZSP]; Villa Colon, 880 m, 26.IV.1936, 5 workers, 2 soldiers, 1 gyne, A. ALFARO [MZSP]; Liberia, 14.I.1930, 150 m, 3 workers, A. ALFARO [MZSP]; 3.5 km NE of Santiago de Pur., San José, 03.VII.1963, 1 gyne, D. H. JANZEN [USNM].

Colombia: Santa Ana, II.1924, 1 worker, 1 soldier, 1 gyne, W. M. MANN [MZSP]. Magdalena: Río Frío, III.1924, 4 workers, 1 soldier, W. M. MANN [MZSP]. Guajira: Serrania de Macuira, 6–8 km S of Nazareth, 70–200 m, 13.VI.1976, 12 workers, 3 soldiers, 1 gyne, 2 males, W. L. BROWN & R. C. KUGLER [MCZC]; Puente Bomba, nr. Dibulla,

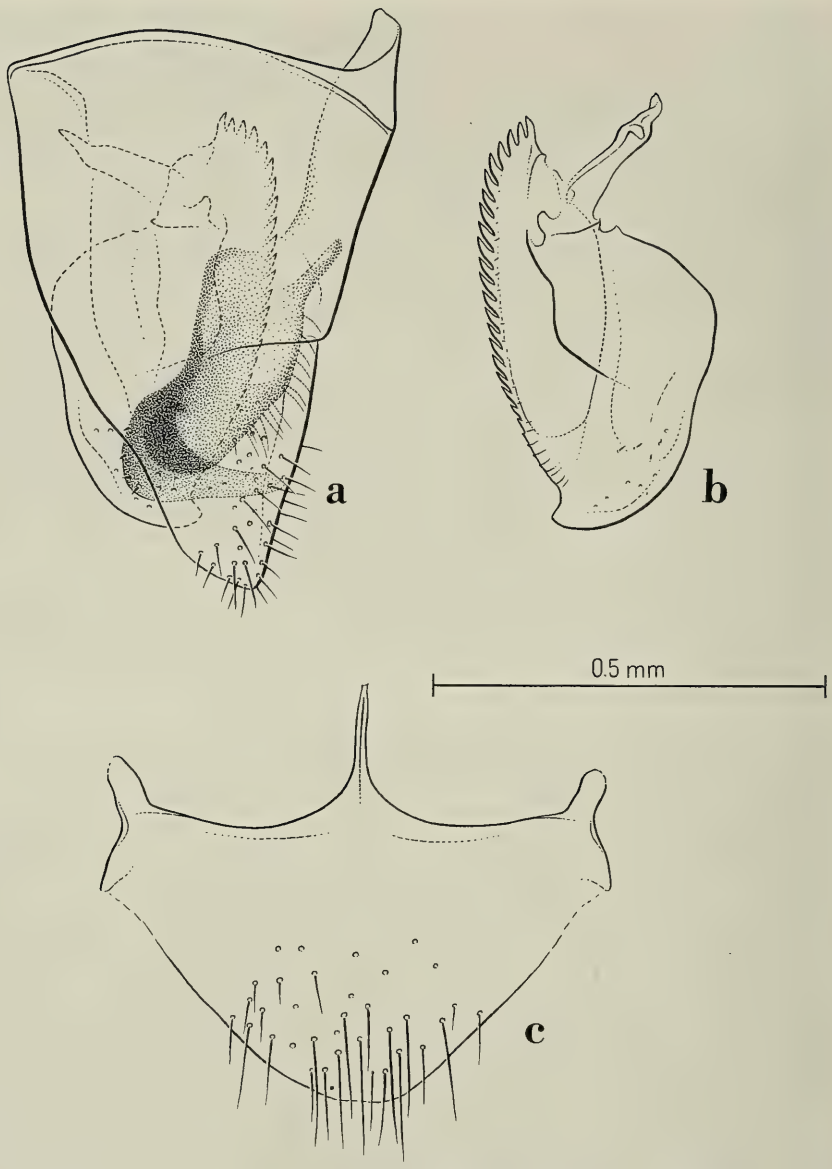


Fig. 234. *Cephalotes pallens* (KLUG). Male from Serrania de Macuira, Colombia. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

19.VI.1976, 5 workers, 1 soldier, 1 gyne, W. L. & D. E. BROWN [MCZC]. M e t a : Carimagua, 370 m, 28.V.1973, 1 gyne, M. L. CORN [MZSP].

St. Vincent: 1 worker (holotype of *araneolus* Smith) [BMNH]; same locality, 1 worker [ZSMC]; same locality, 1 worker, H. H. SMITH [MHNG].

Trinidad & Tobago: T r i n i d a d : Mayaro Bay, 24.XI, 4.XII.1934, 7 workers, 4 soldiers, N. A. WEBER [MCZC]; Nariva Swamp, 05.XII.1934, 7 workers, 3 soldiers, N. A. WEBER [MCZC].

Venezuela: M i r a n d a : Campo Central de Caucagua, 15.III.1982, 1 worker, C. R. F. BRANDÃO et al. [MZSP]. A n z o á t e g u i : 9 km S of Clarines, 02.XI.1986, 1 worker, 1 soldier, CANCELLO, LATTKE & BRANDÃO [MZSP]. B a r r a n c a s : Jan. & Feb. 1935, 18 workers, 1 soldier, 1 gyne, N. A. WEBER [MCZC]. M é r i d a : 30 km SW of Mérida, 02.VI.1976, 1 gyne, A. S. MENKE & D. VINCENT [USNM].

Guyana: no further locality, 1 soldier [MZSP].

Surinam: Distr. Marowijne, 08–29.XII.1963, 2 workers, B. MALKIN [MZSP].

French Guyana: Cayenne [NHMB].

Brazil: A m a z o n a s : no further locality, 2 workers, 3 soldiers, H. W. BATES [MHNG, ZSMC]; Manaus, 1.IX.1962, 15 workers, K. LENKO [MZSP]; same locality, Ponta Negra, 01.IX.1962, 6 workers, 2 soldiers, W. L. BROWN [MCZC]. P a r á : Maracanã, Ilha do Marco, 11–13.I.1993, 2 workers, J. DIAS [MPEG]; Serra Norte, N1 Campo Rupestre, 2–5.IX.1983, 1 worker, R. B. NETO [MPEG]; Serra Cipó Pitanga, 9.XII.1983, 1 gyne, B. MASCARENHAS [MPEG]; São João de Pirabas, Japerica, 16–18.X.1982, 2 workers, J. DIAS [MPEG]; B a h i a : Santo Amaro, ESOMI, 12.XI.1987, 3 workers, E. FERRAZ [CPCC]; Itaberaba, 01–05.XII.1990, 9 workers, 2 males, C. R. F. BRANDÃO et al. [MZSP].

D i s c u s s i o n . - The concavity on the membranaceous expansions of the worker propodeum is much more impressed in small workers than in the larger ones; some small workers may bear another, superficial, anterior notch. This variation makes the small workers of *pallens* appearing more similar to *porrasi* than the large ones. Large workers tend to have the propodeal incision less deep and even almost inexistent in a few cases.

The Mexican specimens intercepted in Texas on *Laelia* and those from San Sebastian are the most distinct among all the material examined. These workers are larger and have broader head, narrower pedicel and the membranaceous expansions of the propodeum simply convex with or without a superficial incision. The associated soldiers from San Sebastian are also very large, the foveae on the disc are denser and the propodeum is narrower than in the other soldiers examined. Only the Guatemalan workers intercepted in New York approach the aforementioned Mexican specimens in size and head width, but they exhibit the usual mesosomal morphology.

FERNÁNDEZ et al. (1996) report this species also from the Colombian state of Huila.

FOREL (1897) reports "*Cryptocerus araneolus*" from Grenada (Lesser Antilles), and, presumably on this sole basis, KEMPF (1972) listed Grenada under the geographic distribution of *pallens*. We did not find specimens from Grenada either in the FOREL collection or in other collections. Kempf's deduction, hence, remains probable but worth of confirmation because of the set of new species similar to *pallens* described in this paper.

D i s t r i b u t i o n : Mexico, Guatemala, St. Vincent (and Grenada?), Costa Rica, Panama, Colombia, Trinidad, Venezuela, Guyanas, Surinam, Brazil.

Cephalotes pellans DE ANDRADE new species

Figs. 235, 236, 237, 238

Cryptocerus pallens KLUG, EMERY, 1896: 635. Male. Nec KLUG, 1824. Misidentification.
Cryptocerus pallens KLUG, FOREL, 1909: 257. Nec KLUG, 1824. Misidentification
Paracryptocerus pallens (KLUG), KEMPF, 1958 a: 153. Partim. Nec KLUG, 1824. Misidentification.

T y p e m a t e r i a l : Holotype soldier from Paraguay labelled: Paraguay, Bohls, in MCSN. Paratypes: 1 worker, 2 gynes and 2 males, same data as the holotype, all MCSN.

D e r i v a t i o n o m i n i s : *pellans* is an anagram of *pallens*, the name of the species with which this one had been previously confused.

D i a g n o s i s . - A member of the *pallens* clade differing from its sister species *decoloratus*, in the worker, by the following characters: petiole with a pair of spines 1.3 times longer than the maximum petiolar length and HBaI > 47, and, in the soldier and in the gyne, foveae on disc sparser.

W o r k e r (Fig. 235). - Differing from *decoloratus* in the following characters. Pronotum narrower. Margin of the lateral expansions of the mesosoma minutely crenulate. Membranaceous expansions of the propodeum with or without superficial notch. Peduncular spines longer and more pointed. Gaster more elongate, its anterior expansions protruding more anteriorly, narrowing backwards, surpassing the anterior half and continuing as a thin margin until the posterior border. Mid and hind basitarsi shorter and broader.

Sculpture. Head and mesosoma with foveae denser and separate by irregular, longitudinal rugosities. Frontal carinae with less impressed foveae and with thin, longitudinal rugosities. Pleurae with thin, longitudinal rugosities, more impressed on the propleurae. Anterior third and sides of the first gastral tergite reticulate, with dense, very superficial foveae and with thin, longitudinal rugosities.

Colour. Dark brown to black with lighter membranaceous expansions.

Measurements (in mm) and indices: TL 3.28–4.86; HL 0.76–1.10; HW 0.92–1.26; EL 0.19–0.28; PW 0.76–1.08; PeW 0.60–0.92; PpW 0.52–0.68; HBaL 0.22–0.26; HBaW 0.11–0.13; CI 114.5–121.6; PI 116.7–123.1; PPeI 117.4–129.9; PPpI 141.8–158.8; HBaI 50.0–52.0.

S o l d i e r (Fig. 236). - Differing from *decoloratus* in the following characters. Head disc longer. Center of the disc only occasionally weakly convex. Mesosoma narrower. Mesonotal sides with or without an additional pair of minute denticles. Pedicel narrower and with shorter spines. Gaster more oval and with a pair of more protruding lobes.

Sculpture. Head dorsum minutely, superficially punctate, shining and with small, sparse foveae. Some specimens have the head dorsum covered by a very thin layer of probable camouflage material. Sculpture on the sides of the disc less dense. Ventral part of the head shining, with thin, longitudinal rugosities behind the eyes, smooth in the middle and with shallow, small foveae separated by irregular, longitudinal rugosities on the sides. Propleurae with thin, irregular, slightly transversal rugosities. First gastral tergite with more superficial and more irregular foveae separate by longitudinal, thin rugosities on the anterior third only; in some specimens the rugosities prolonging up to the posterior half.

Pilosity. As in *decoloratus* except some specimens with rare, short, clubbed hairs on the pronotal sides.

Colour. Dark brown to black with lighter gaster.

Measurements (in mm) and indices: TL 6.60–7.40; HL 1.80–2.16; HW 1.60–1.78; EL 0.39–0.41; PW 1.56–1.70; PeW 0.78–0.80; PpW 0.70–0.72; HBaL 0.27–0.34; HBaW 0.15–0.16; CI 82.7–87.2; PI 101.2–109.7; PPeI 195.0–215.2; PPpI 222.8–239.4; HBaI 47.0–55.6.

G y n e (Fig. 237). - Differing from the soldier in the following characters. Sides of the disc with lower border. Floor of the disc flat or gently convex medially. Vertex with a small, superficial concavity. Vertexal angles less protruding than in the soldier. Humeral angles with a pair of obtuse or nearly round teeth. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly gently convex and posteriorly with a pair of broad, almost round teeth separate by a deep incision. Anterior face of the petiole oblique, anterior border concave. Petiolar sides with or without a minute pair of denticles medially. Postpetiole as in the soldier but with the lateral spines shorter, truncate or pointed.

Gaster. As in the soldier but much longer. Legs as in the soldier.

Sculpture. Head dorsum superficially and minutely punctate and with variably clumped foveae missing on the anterior third of the head dorsum of some specimens. Propleurae with thin, irregular, slightly transversal rugosities. Upper and ventral part of the lower metapleurae with dense, small foveae.

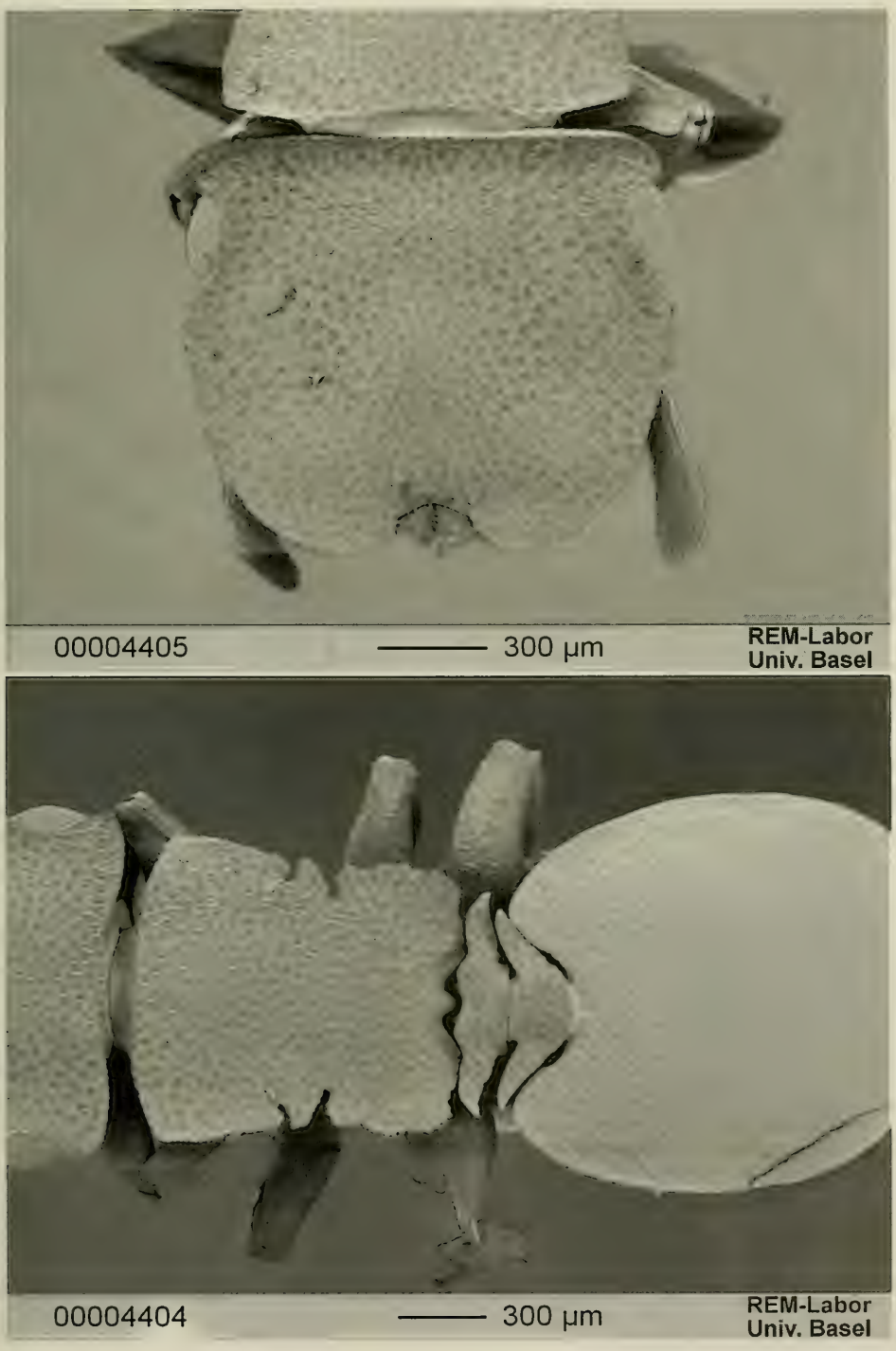


Fig. 235. *Cephalotes pellans* DE ANDRADE. Worker from Três Lagoas (Mato Grosso do Sul), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

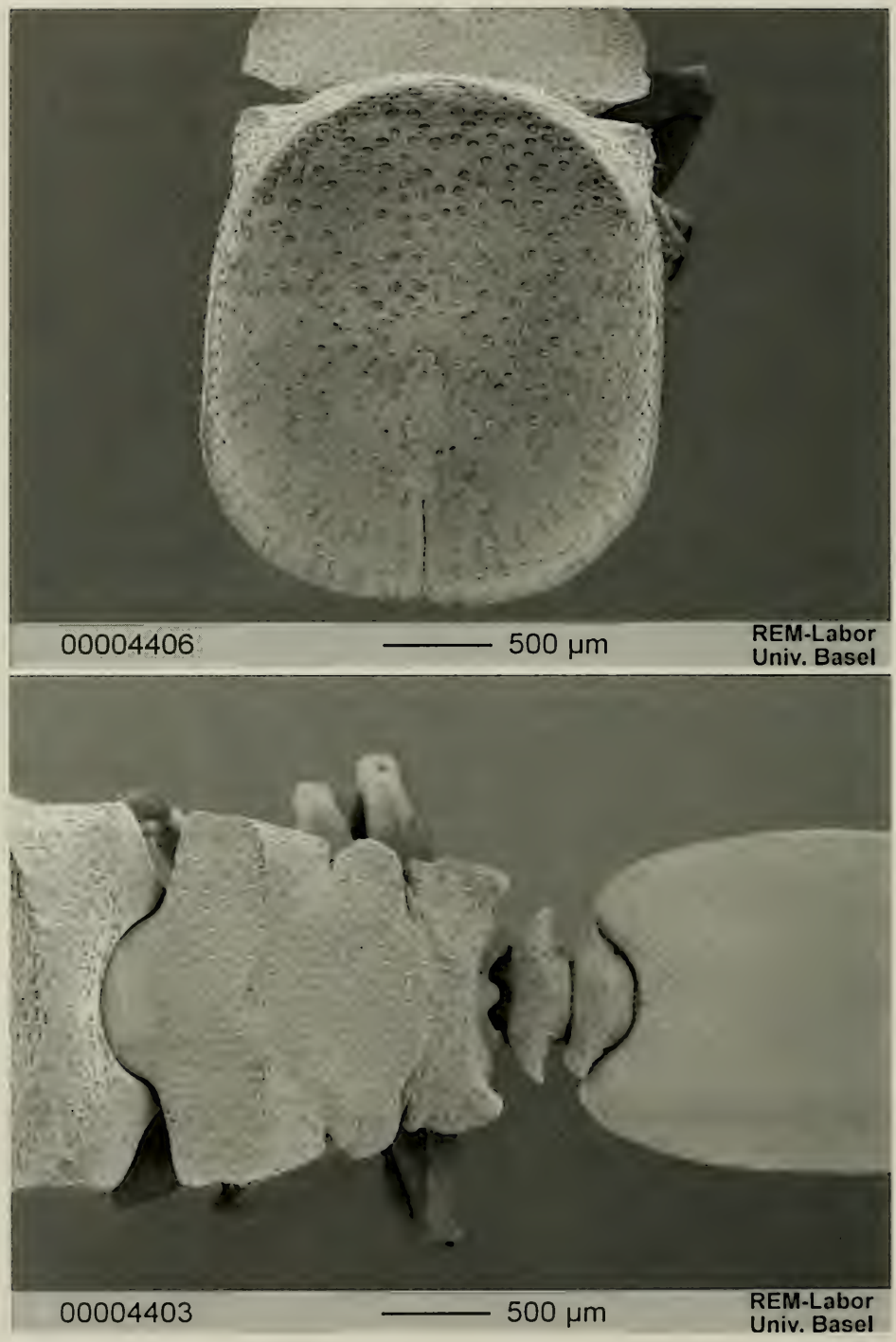


Fig. 236. *Cephalotes pellans* DE ANDRADE. Soldier from Três Lagoas (Mato Grosso do Sul), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

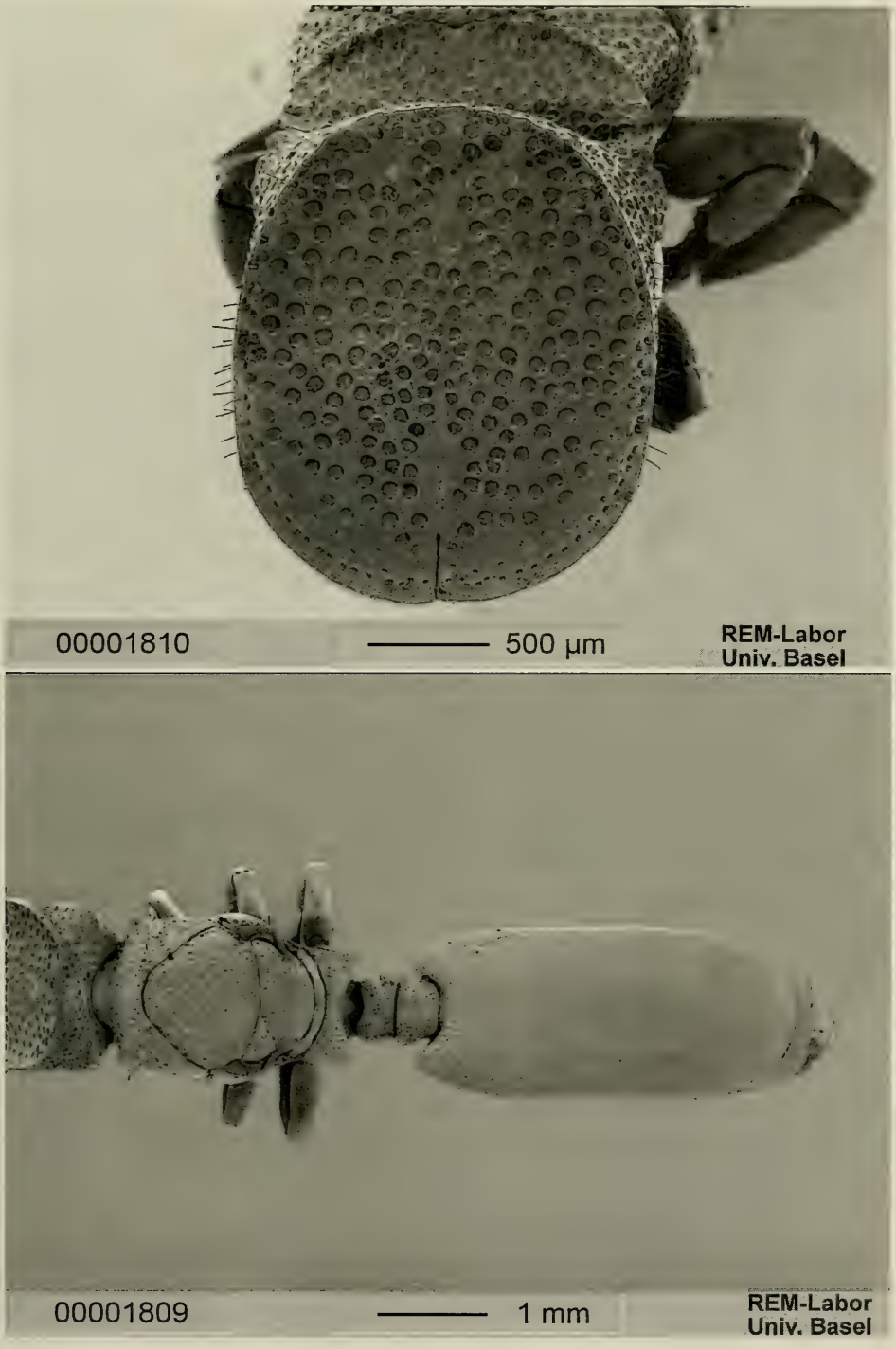


Fig. 237. *Cephalotes pellans* DE ANDRADE. Gyne from Utiariti (Mato Grosso), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Pilosity. As in the soldier except the sides of the mesosoma with rare, long, clubbed hairs as those on the sides of the disc.

Colour. As in the soldier.

Measurements (in mm) and indices: TL 8.52–8.68; HL 1.80–1.88; HW 1.56–1.68; EL 0.42–0.43; PW 1.44–1.58; PeW 0.58–0.62; PpW 0.70–0.73; HBaL 0.40–0.43; HBaW 0.17–0.19; CI 86.7–89.4; PI 102.6–111.1; PPeI 234.9–254.8; PPpI 200.0–217.1; HBaI 41.9–44.2.

Male. - Differing from *varians* in the following characters. Frontal carinae lower. Clypeus less convex posteriorly and not incised anteriorly. Mesosoma. Pronotum in dorsal view with the sides superficially marginate. Wings more infuscate and darker.

Genitalia and subgenital plate as in Fig. 238.

Sculpture. Head dorsum minutely reticulate and with variably clumped foveae separate by thin, irregularly longitudinal rugosities, oriented transversally in front of the eyes and between the scapes. Ventral part of the head reticulate and with foveae separate by slightly longitudinal rugosities. Pronotum, mesonotum and scutellum with superficial, minute reticulation and with foveae as on the head dorsum, shallower, sparser and separate by thin, longitudinal rugosities on the mesonotum and on the scutellum. Basal face of the propodeum reticulate and with irregular foveae and longitudinal rugosities. Pedicel and propleurae eticulate and sometimes with few superficial foveae and short rugosities on the sides of the petiole and postpetiole and on the upper part of the propleurae. Mesopleurae reticulate and with thin, longitudinal rugosities on the posterior half, covered by superficial foveae on the center of the lower and upper mesopleurae. Metapleurae reticulate and irregularly rugose; upper part of the metapleurae with few, irregular foveae. Gaster superficially reticulate and subopaque to shining. Legs punctate, with moderately shining femora.

Pilosity. Body with long, thin, flexuous, pointed, golden hairs, dense on the head, on the mesosoma and on the pedicel, sparser on the gaster and on the femora. Gaster and legs with similar hairs but shorter, appressed on the tergites, decumbent on the sternites and on the femora. Tibiae and tarsi with short, pointed hairs.

Colour. Dark brown to black with slightly lighter coxae, proximal part of the femora, and gaster. Legs yellowish with darker tarsomeres.

Measurements (in mm) and indices: TL 4.84–4.92; HL 0.76; HW 0.92; EL 0.39–0.40; PW 0.85–0.88; PeW 0.40–0.42; PpW 0.44–0.46; HBaL 0.43–0.47; HBaW 0.09; CI 121.0; PI 104.5–108.2; PPeI 202.4–220.0; PPpI 184.8–200.0; HBaI 19.1–20.4.

Material examined. - **Brazil**: Mato Grosso: no further locality, 1886, 2 workers, 3 gynes, P. Germain [MCSN, MNHN]; Utiariti, 325 m, Rio Papagaio, VII.1961, 42 workers, 3 soldiers, 5 gynes, 1 male, K. Lenko [MZSP]; same locality, 30.X.1966, 1 gyne, Lenko & Pereira [MZSP]; Sinop, 55°37' W, 12°31' S, X.1974, 5 workers, 1 soldier, M. Alvarenga [MZSP]. Mato Grosso do Sul: Três Lagoas, 24.V.1964, 33 workers, 14 soldiers, Exp. Dep. Zool. [MZSP]; same locality, Fazenda do Cervo, 15–18.IX.1964, 5 workers, 1 soldier, Exp. Dep. Zool. [MZSP]; same locality, Fazenda Beija Flor, 25.V.1964, 1 soldier, Exp. Dep. Zool. [MZSP]; same locality, Fazenda Canaã, 15.X.1966, 1 worker, 1 gyne, F. Lane [MZSP]; same locality, left side of Rio Sucuriu, Fazenda Canaã, X.1966, 1 soldier, 1 gyne, F. Lane [MZSP]; Corumbá, Serra do Urucum, 27.X & 26.XI.1960, 2 gynes [MZSP]. Minas Gerais: Cáceres, 15–18.X.1961, 1 soldier, F. M. Oliveira [MZSP]; Poconé, V.1948, 3 workers, 1 soldier, C. Valette [MZSP]. São Paulo: Bálsamo, 8.VII.1972, 2 workers, 1 soldier, J. M. Diniz [MZSP]; Cajuru, Fazenda Santa Carlota, 21°17' S, 47°18' W, 12.VI. & 31.XII.1992, 22.II & 24.IV.1993, 13.X.1994, 29 workers, 1 soldier, R. Silvestri [MZSP]; Nova Europa, Fazenda Itaquerê, 25.VIII.1965, 75 workers, 10 soldiers, 1 male, K. Lenko [MZSP]; Mogi-Guaçu, Fazenda Campininha, 16.XII.1978, 1 gyne, H. C. M. [MZSP]; Agudos, 28.IX.1953, 1 worker, W. W. Kempf [MZSP]; same locality, Jul. and Aug. 1954, May 1958, 5 workers, R. Mueller [MZSP]; same locality, 02.XI.1953, 8 workers, 4 soldiers, 3 gynes, 8 males, O. Ludovic [MZSP].

Bolivia: Beni: Rurrenabaque, Oct. 1921, 2 workers, 1 soldier, W. M. Mann [MZSP].

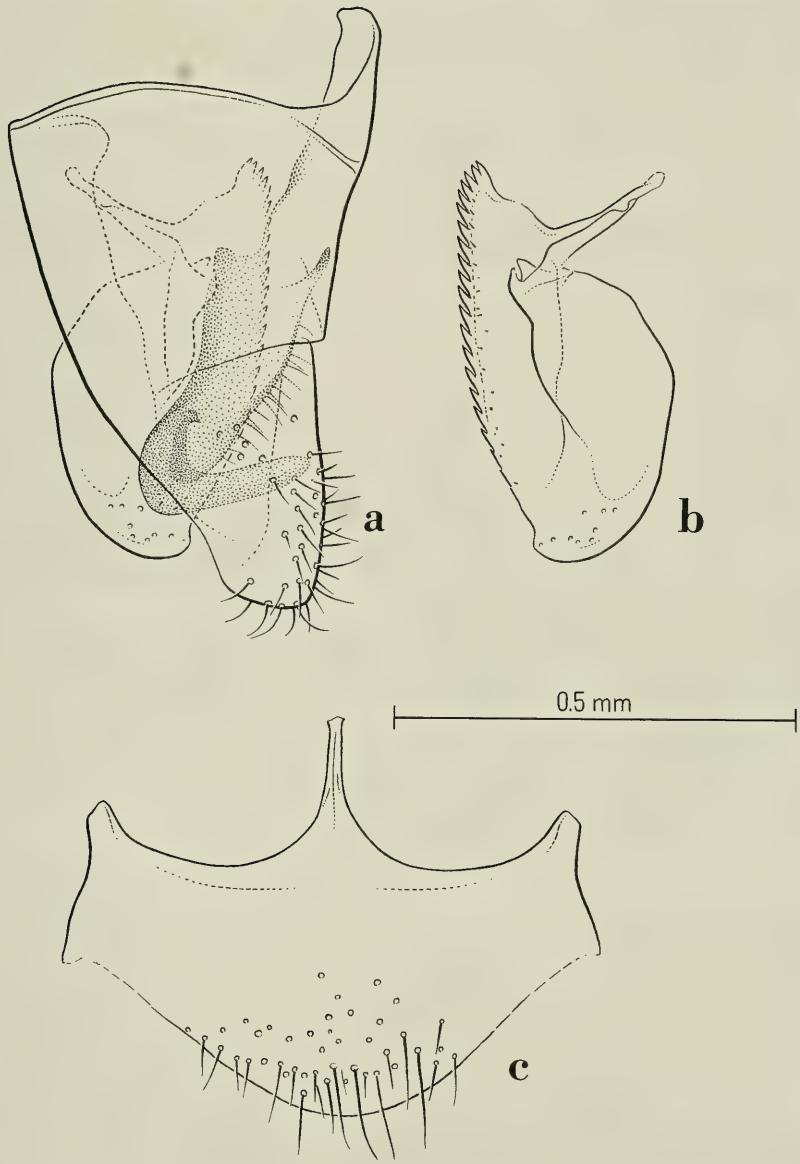


Fig. 238. *Cephalotes pellans* DE ANDRADE. Male from Utiariti (Mato Grosso), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Paraguay: no further locality, 1 worker (paratype), 1 soldier (holotype), 2 gynes (paratypes), 2 males (paratypes), BOHLS [MCSN]. Presidente Hayes: Laguna Pora, 60 km NE of Filadelfia, 12.X.1978, 1 worker, 1 soldier, K. H. REDFORD [MCZC]. La Cordillera: San Bernardino, 2 gynes, K. FIEBRIG [MHNG, ZSMC].

Discussion. - *C. pellans* is another species separated in this paper and previously confused, together with seven others, under the name *pallens*.

In this species we examined miniature workers with a maximum length of 3.3 mm from different localities. Similar miniature workers are unknown among other, related species, except *pallens*, where they appear, nonetheless, to be less frequent.

There are also small soldiers and gynes with foveae on the disc denser than in the larger ones.

It is possible that the presence of these variation trends contributed to the former failures to distinguish the species of this clade, but none of the characters subject to individual variability examined by us affects the specific apomorphies listed in the diagnosis.

D i s t r i b u t i o n : Brazil, Bolivia and Paraguay.

Cephalotes decoloratus DE ANDRADE new name and new status
Figs. 239, 240

Cryptocerus varians marginatus WHEELER & MANN, 1914: 39, figs. 17 a-b. Worker, soldier and gyne. Original description. Nec *Cryptocerus marginatus* FABRICIUS, 1804. Type locality: restricted to Diquini (Haiti) by KEMPF, 1958 a: 152. Type material: 1 worker and 2 soldiers labelled as lectotype by Kempf and 3 additional workers labelled as paratype [MZSP], 1 soldier and 1 worker [MHNG], 2 workers, 1 soldier [MCSN], 2 workers and 1 soldier [MCZC], 3 workers [NHMB], 10 workers, 5 soldiers [USNM]; additional original type material from Manneville (Haiti), 2 workers and 1 soldier [MCZC], 3 workers [MHNG], 4 workers and 2 soldiers [NHMB], 2 workers and 1 soldier [MZSP]; additional type material from Petionville (Haiti), 2 workers, 1 soldier [MZSP], 1 worker [USMN], all examined.

Paracryptocerus pallens (KLUG), KEMPF, 1958 a: 151. Partim. Nec KLUG, 1824. Misidentification.

D e r i v a t i o n o m i n i s : in Latin *decoloratus* (= pale) is a synonym of *pallens*, the name of the species with which the present one had been previously confused.

D i a g n o s i s . - A member of the *pallens* clade differing from its sister species *pellans* by the following characters: worker petiole with a pair of spines shorter than its length and gaster anteriorly with a pair of broad, round membranaceous borders; soldier and gyne with deeper and denser foveae on the head disc.

W o r k e r (Fig. 239). - Head broader than long. Vertexal angles with a pair of narrow, round membranaceous expansions.

Mesosoma. Scapular angles not visible in dorsal view. Anterior pronotal border convex. Pronotum with a pair of broad membranaceous expansions gently converging posteriorly. Promesonotal suture variably impressed. Mesonotal sides with a pair of triangular semimembranaceous teeth followed or not by a pair of minute denticles. Propodeum with poorly differentiated basal and declivous faces. Membranaceous expansions of the propodeum with one or, rarely, two pairs of superficial incisions. Margin of the propodeal expansions minutely crenulate.

Petiole with the anterior face truncate and medially slightly concave. Petiolar sides with triangular, pointed spines. Postpetiole convex dorsally; its sides with pointed or round spines directed forwards at the base.

Gaster suboval, not strongly protruding anteriorly and with a pair of round, membranaceous expansions surpassing the stigma posteriorly and continuing backwards up to the posterior border as a thin margin.

Mid and hind femora gently angulate and crested; the crest narrower on the mid femora. Mid and hind basitarsi flat, with the proximal part broader than the distal one.

Sculpture. Head dorsum, mesosoma and pedicel minutely reticulate and with dense foveae; the foveae deeper on the posterior third of the head, shallower, smaller and irregular on the

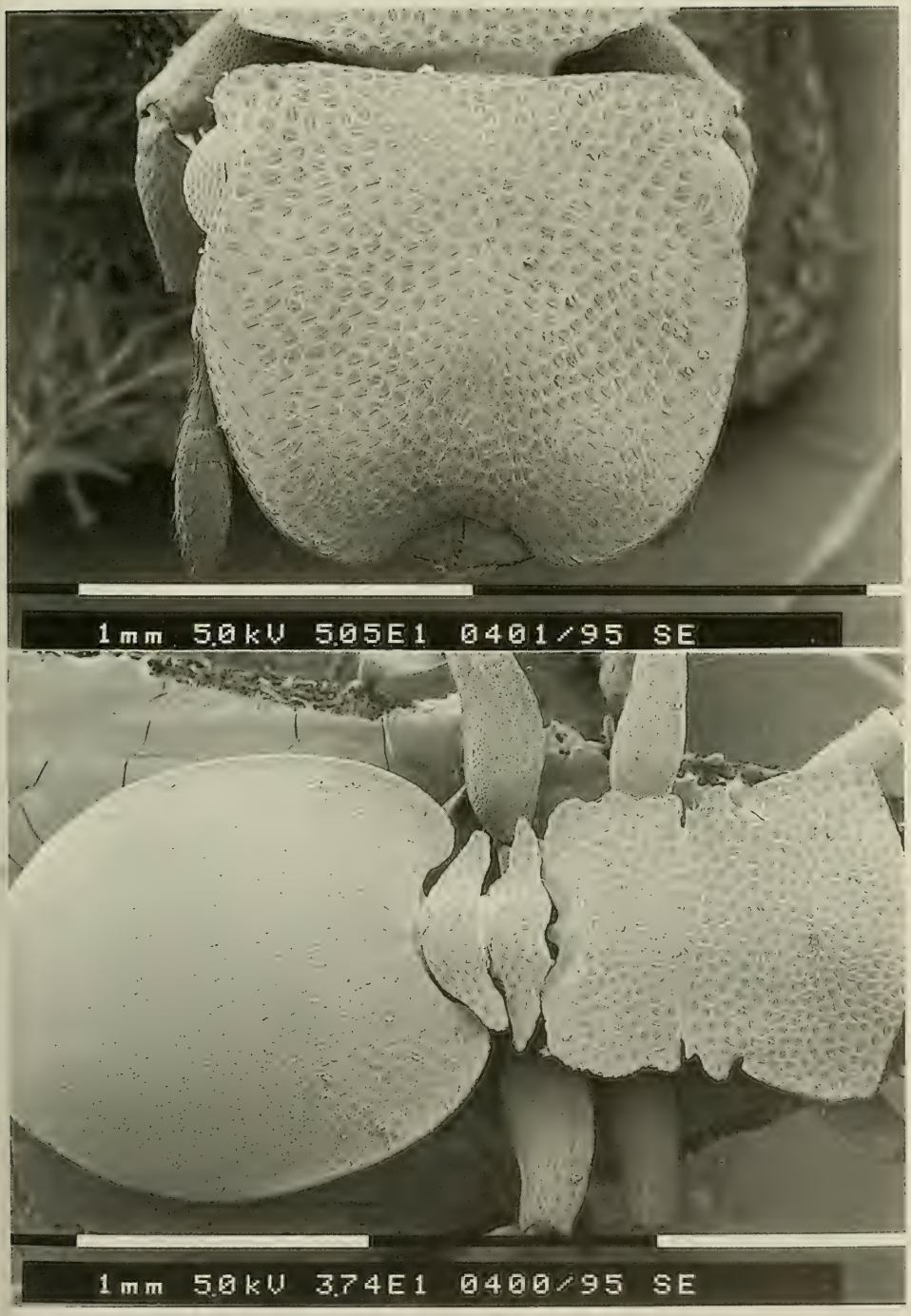


Fig. 239. *Cephalotes decoloratus* DE ANDRADE. Worker from Bani, Dominican Republic: head (top) and meso- and metasoma (bottom) in dorsal view.

anterior third, sparser and superimposed to short, thin, irregular rugosities on the frontal carinae and very small on the pedicel. Ventral part of the head posteriorly reticulate; this sculpture more superficial and superimposed to foveae and longitudinal rugosities on the remaining ventral surface. Pleurae reticulate and with thin, faint longitudinal rugosities on the propleurae. First gastral tergite reticulate and with sparse, superficial foveae larger on the anterior third and on the sides; thin, superficial, irregular rugosites superimposed to this sculpture. First gastral sternite with sculpture similar to the one on the corresponding tergite but less impressed. Center of the first gastral sternite superficially shining. Legs reticulate with sparse, small, very superficial and slightly irregular foveae, denser on the outer face of the tibiae.

Pilosity. Each fovea with an appressed hair. Sides of the vertexal angles, posterior borders of the gastral tergites and sternites, and legs with rare clubbed hairs; similar hairs but thinner and denser on the first gastral sternite. Parts of the gaster and legs without foveae with short, appressed, very thin hairs. Gastral sternites with additional, rare, long, pointed hairs.

Colour. Brown to black with the membranaceous expansions of the body lighter.

Measurements (in mm) and indices: TL 4.50–4.72; HL 1.04–1.10; HW 1.28–1.34; EL 0.27–0.28; PW 1.06–1.14; PeW 0.73–0.78; PpW 0.65–0.70; HBaL 0.31–0.33; HBaW 0.13–0.14; CI 121.8–123.1; PI 117.5–120.7; PPeI 145.2–146.1; PPpI 162.8–163.1; HBaI 41.9–42.4.

S o l d i e r (Fig. 240). - Head disc suboval with strongly raised sides. Floor of the disc weakly convex medially. Vertex superficially impressed. Vertexal angles completely separate from the disc, obtuse or pointed and with the margin variably crenulate. Eyes slightly convex and hidden by the disc. Mandibles laterally carinate.

Mesosoma. Humeral angles with a pair of obtuse teeth. Mesonotum with a pair of broad, truncate or obtuse teeth followed or not by a pair of minute denticles. Sides of the basal face of the propodeum with two pairs of round swellings or teeth followed by another pair of stout teeth curved up and forwards. Declivous face of the propodeum narrowing posteriorly.

Pedicel as in the worker but with narrower and shorter spines.

Hind femora gently angulate and strongly carinate.

Gaster. Oval and with a pair of protruding anterior lobes.

Sculpture. Head dorsum minutely punctate variably shining and with large, differently clumped foveae diminishing in size anteriorly, larger and deeper posteriorly. Few specimens have parts of the head covered by a thin layer of probably camouflage material. Sides of the disc densely and irregularly foveolate, the foveae more superficial on the anterior half. Ventral part of the head shining, punctate, irregularly foveolate-rugulose; the foveae and rugosities absent on the posterior sides. Mesosoma minutely reticulate-punctate and with dense foveae, sparser on the pronotum and smaller on the propodeum. Pedicel with sculpture similar to the one on the propodeum but with smaller and less regular foveae. Pleurae reticulate. Propleurae with shallow foveae on the upper part; smaller specimens with the foveae sparser and superimposed to few transversal, thin rugosities. Gaster and legs with sculpture similar to the one of the worker but with slightly larger foveae.

Pilosity. Each fovea with an appressed hair. External border of the disc and sides of the head with few, suberect, long, clavate hairs, absent on the anterior border of the disc. Internal border of the disc with one or two rows of long, appressed hairs. Vertexal angles and posterior border of the gastral segments with clubbed hairs, rare and shorter on the vertexal angles; First gastral sternite with rare, thin clubbed hairs. Parts of the gaster and legs without foveae with short, appressed hairs. Gastral sternites with additional, rare, long, pointed hairs.

Colour. Dark brown to black with slightly lighter gaster.

Measurements (in mm) and indices: TL 6.52–7.66; HL 1.80–2.16; HW 1.72–2.00; EL 0.35–0.36; PW 1.62–1.84; PeW 0.77–0.86; PpW 0.69–0.79; HBaL 0.30–0.36; HBaW 0.15–0.17; CI 92.6–95.5; PI 106.2–108.7; PPeI 210.4–213.9; PPpI 232.9–234.8; HBaI 47.2–50.0.

G y n e . - Differing from the soldier in the following characters. Sides of the disc with lower border. Floor of the disc flat. Posterior part of the disc superficially depressed. Humeral angles obtuse. Pronotal crest less marked. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly convex and posteriorly with a pair

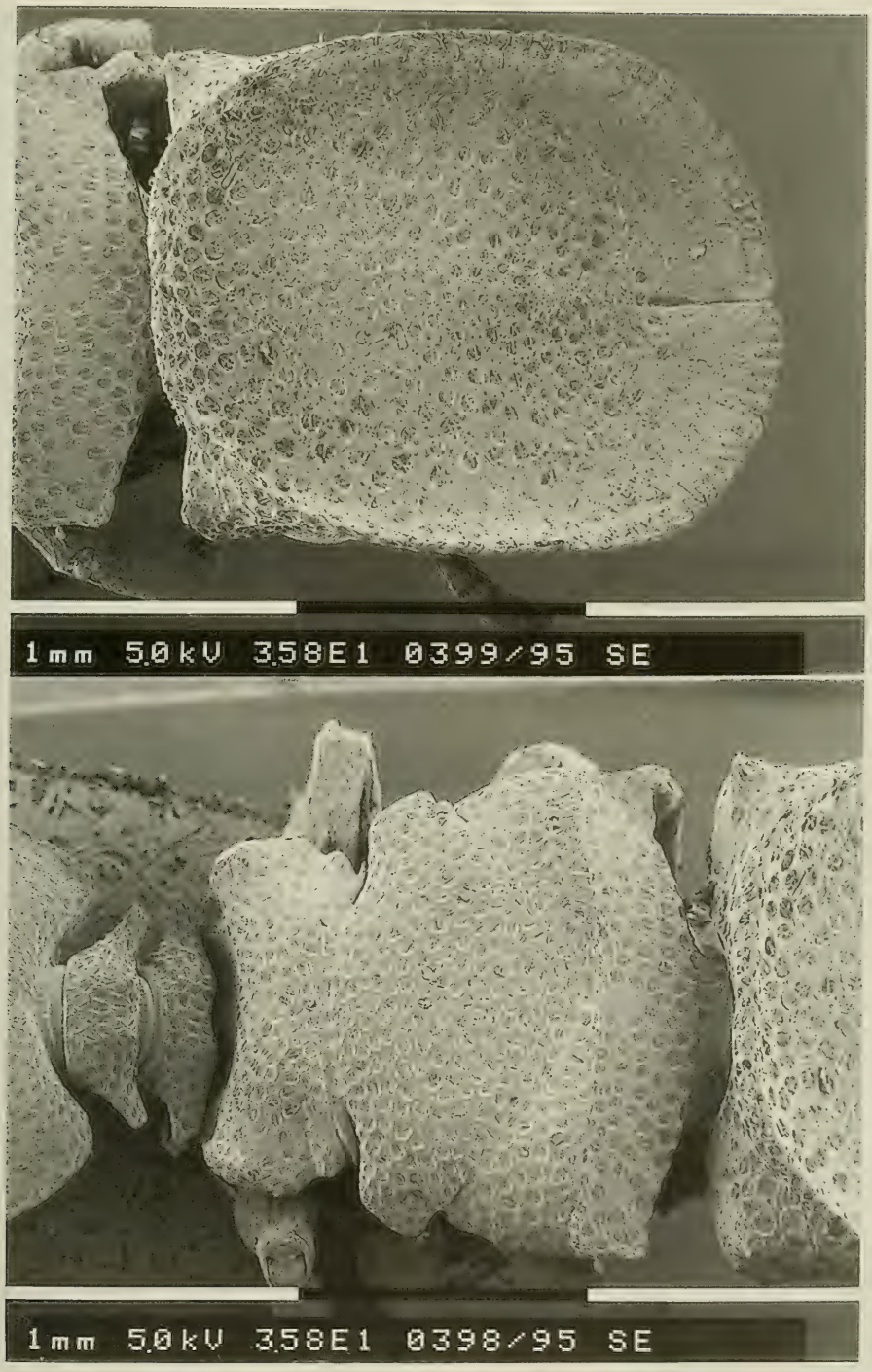


Fig. 240. *Cephalotes decoloratus* DE ANDRADE. Soldier from Bani, Dominican Republic: head (top) and mesosoma (bottom) in dorsal view.

of broad, obtuse teeth separate by a deep, marked incision. Anterior face of the petiole more oblique. Petiolar sides with a pair of minute denticles. Postpetiole as in the soldier but with the spines broader, shorter and slightly more pointed. Gaster as in the soldier but much longer. Legs as in the soldier but with less salient carinae on the outer face of the femora.

Sculpture. Foveae deeper and denser on the head dorsum, larger and shallower on the mesosoma, sparse, superficial on the propleurae, small, dense, and deep on the upper and anterior half of the lower mesopleurae.

Pilosity. As in the soldier.

Colour. Apparently brown but all specimens available are immature.

Measurements (in mm) and indices: TL 8.32–8.36; HL 1.80; HW 1.60; EL 0.42–0.44; PW 1.54–1.52; PeW 0.67–0.71; PpW 0.76–0.77; HBaL 0.49–0.48; HBaW 0.20; CI 88.8; PI 103.9–105.3; PPeI 214.1–229.8; PPpI 197.4–202.6; HBaI 40.8–41.7.

Material examined. - **Haiti**: Diquini, 1 worker and 2 soldiers on the same pin (labelled as lectotype by Kempf; we find no published trace of this designation) [MZSP], 3 workers (labelled as paratypes by Kempf) [MZSP], 18 workers, 8 soldiers (syntypes) W. M. Mann [MHNG, USNM, MCZC]; Manneville, 11 workers, 4 soldiers (all syntypes), W. M. Mann [MCSN, MCZC, MHNG, NHMB]; Petionville, 3 workers, 1 soldier (syntypes), W. M. Mann [MZSP, USNM]; same locality, 16–17.XI.1934, 9 workers, Darlington [MCZC]; Trou Caiman, 15–20.XI.1934, 1 worker, Darlington [MCZC].

Dominican Republic: Bani, 65 m, different dates in 1971 and 1972, 27 workers, 13 soldiers, 4 gynes, J. &. S. Klapperich [CPCC, NHMB]; Prov. Pedernales, 14 km N Cabo Rojo, 150 m, 19.VIII.1988, 1 worker, M. A. Ivie et al. [USNM].

Discussion. - *C. decoloratus* is endemic from Hispaniola. This species had been previously described by Wheeler & Mann (1914) as a subspecies of *varians* using a preoccupied name.

Its sister species is *pellans* from S. Brazil. The characters distinguishing the two species and already listed in the diagnosis are constant among all 71 workers, 27 soldiers and 4 gynes we examined. This fact, together with the geographic distance between the two, leaves no doubt on the necessity to consider *decoloratus* as a good species.

The most significant variation observed in *decoloratus* is in the soldiers from Bani: these soldiers have the floor of the disc with foveae shallower and sparser than those from Haiti.

Distribution: Hispaniola.

Cephalotes decolor de Andrade new species
Figs. 241, 242

Paracryptocerus pallens (Klug), Kempf, 1958 a: 151. Partim. Nec Klug, 1824. Misidentification.

Type material: Holotype soldier from Venezuela labelled: Pq. Nac. Mochima, Sucre, 50 m, 02.X.1986, E. Cancello & C. R. F. Brandão. Paratypes 16 workers and 3 soldiers, same data as the holotype, all MZSP.

Derivatio nominis: in Latin *decolor* is a synonym of *pallens*, the name of the species with which the present had been previously confused.

Diagnosis. - A member of the *pallens* clade differing from *decoloratus* and *pellans*, by the following combination of characters: worker only, frontal carinae superficially and irregularly rugulose-foveolate, propodeal sides with a pair of convex,

membranaceous expansions, petiole with a pair of broad, pointed spines shorter than the maximum petiolar length, gaster anteriorly protruding, anterior third and sides of the first gastral tergite covered by dense foveae; soldier and gyne, sides of the disc with dense, clubbed hairs, head dorsum without protruding tumulus; soldier only, antennal scrobes reaching at most the anterior border of the eyes, dorsum of the head with superficial, sparse, small foveae, and floor of the disc with foveae bearing appressed hairs; gyne only, head dorsum with dense, superficial foveae and CI > 96.0.

W o r k e r (Fig. 242). - Head broader than long. Vertexal angles with a pair of narrow, round or obtuse membranaceous expansions.

Mesosoma. Anterior pronotal border convex. Anterior pronotal border with a pair of narrow, membranaceous distal expansions forming an obtuse angle with the pronotal sides. Pronotal sides with a pair of broad membranaceous expansions converging posteriorly. Promesonotal suture, in dorsal view, superficially impressed in some specimens only. Mesonotum with a pair of triangular teeth. Propodeum with weakly differentiate basal and declivous faces and completely surrounded by a pair of broad, convex, membranaceous expansions with a crenulate margin in some specimens only. Propodeal suture impressed.

Petiole. Anterior face truncate and slightly concave medially. Petiolar sides with a pair of broad, triangular, pointed spines. Postpetiolar node convex dorsally; postpetiolar sides with a pair of pointed spines directed forwards at the base.

Gaster. Oval, strongly protruding anteriorly and with a pair of membranaceous expansions surpassing the stigma posteriorly and continuing as a thin margin backwards.

Hind femora gently angulate, cristate and carinate on most of their length. Mid femora gently angulate and superficially bicarinate. Mid and hind basitarsi flat, narrowing distally.

Sculpture. Head and mesosoma minutely reticulate and with superficial, dense foveae, shallower and smaller on the anterior part of the head, sparser on the frontal carinae, deeper on the vertex and on the mesosoma. Ventral part of the head reticulate in its posterior third and only superficially reticulate-foveolate in the two anterior thirds, the foveae separate by thin, irregular, longitudinal rugosities. Foveae on the mesosoma separate by irregular, longitudinal rugosities in some specimens only. Pedicel with sculpture similar to the one of the mesosoma but with shallower and smaller foveae. Pleurae reticulate and with thin, longitudinal rugosities. Gaster reticulate. First gastral tergite foveolate on the anterior third and on the sides, the foveae separate by thin, irregular, longitudinal rugosities. First gastral sternite with similar to the corresponding tergite but with less regular foveae. Center of the first gastral sternite minutely and sparsely punctate and shining. Legs reticulate with sparse, irregular, superficial foveae, smaller and dense on the outer face of the tibiae.

Pilosity. Each fovea with an appressed hair. Sides of the frontal carinae and of the vertexal angles, posterior borders of the gastral tergites, sternites and legs with rare clubbed hairs, denser on the first gastral sternite. Parts of the gaster and legs without foveae with short, appressed, thin hairs. Gastral sternites with additional rare, long, pointed hairs.

Colour. Dark brown to black with the membranaceous expansions lighter.

Measurements (in mm) and indices: TL 5.04–5.76; HL 1.14–1.32; HW 1.36–1.54; EL 0.30–0.32; PW 1.10–1.44; PeW 0.89–1.00; PpW 0.77–0.88; HBaL 0.35–0.39; HBaW 0.15–0.16; CI 116.7–119.3; PI 106.9–113.3; PPeI 134.8–144.0; PPpI 155.8–163.6; HBaI 41.0–41.6.

S o l d i e r (Fig. 242). - Head slightly broader than long. Sides of the disc strongly raised. Floor of the disc gently convex medially. Vertexal angles completely separate from the disc, obtuse and with crenulate margin. Eyes slightly convex and hidden by the disc. Mandibles laterally carinate.

Mesosoma. Humeral angles with a pair of obtuse teeth. Pronotal sides gently convex and slightly converging posteriorly. Pronotal crest marked and interrupted only medially. Pronotal suture in dorsal view superficially impressed medially and more impressed laterally. Promesonotal suture impressed. Mesonotal sides with a pair of broad, truncate teeth.

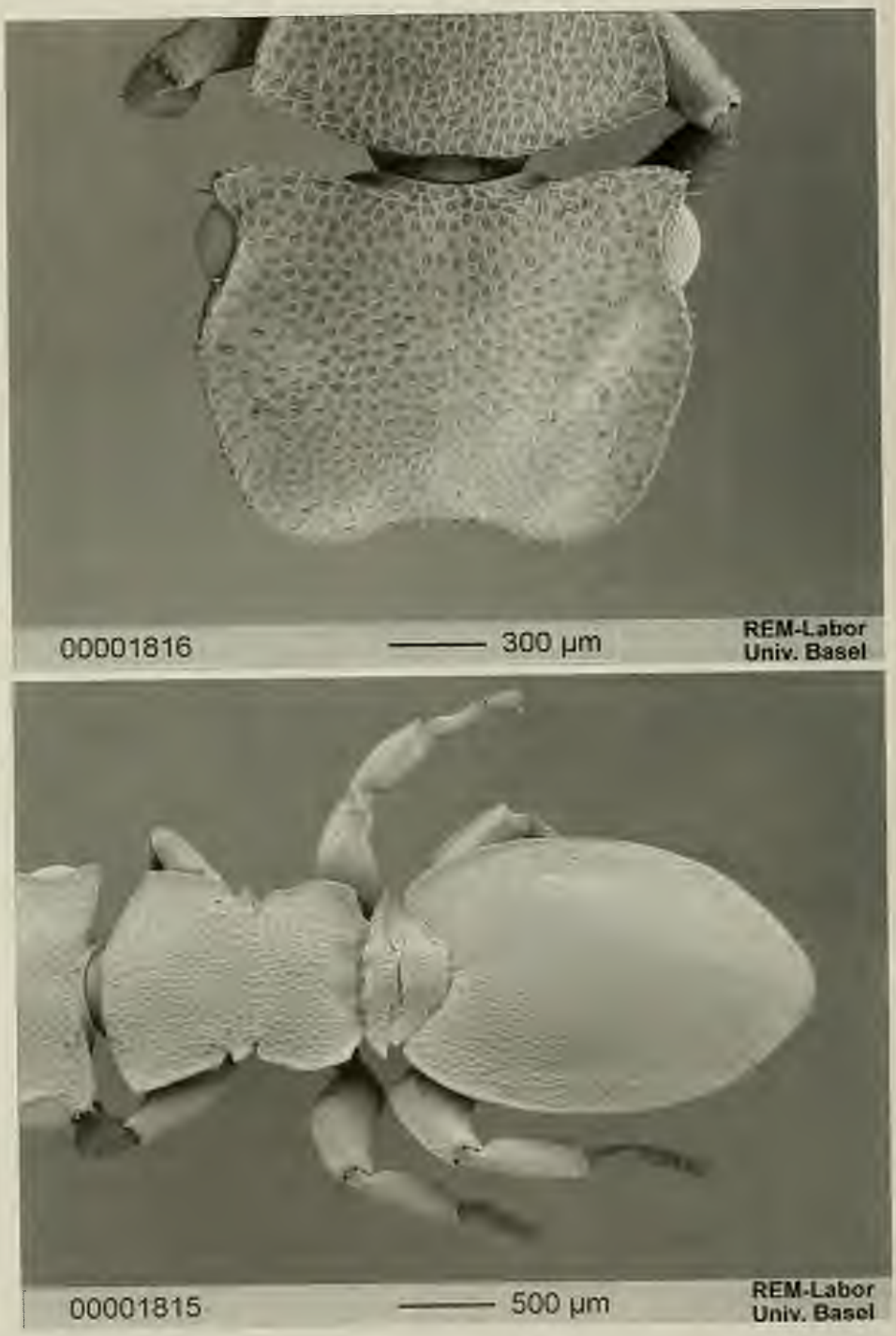


Fig. 241. *Cephalotes decolor* DE ANDRADE. Worker from Venezuela (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

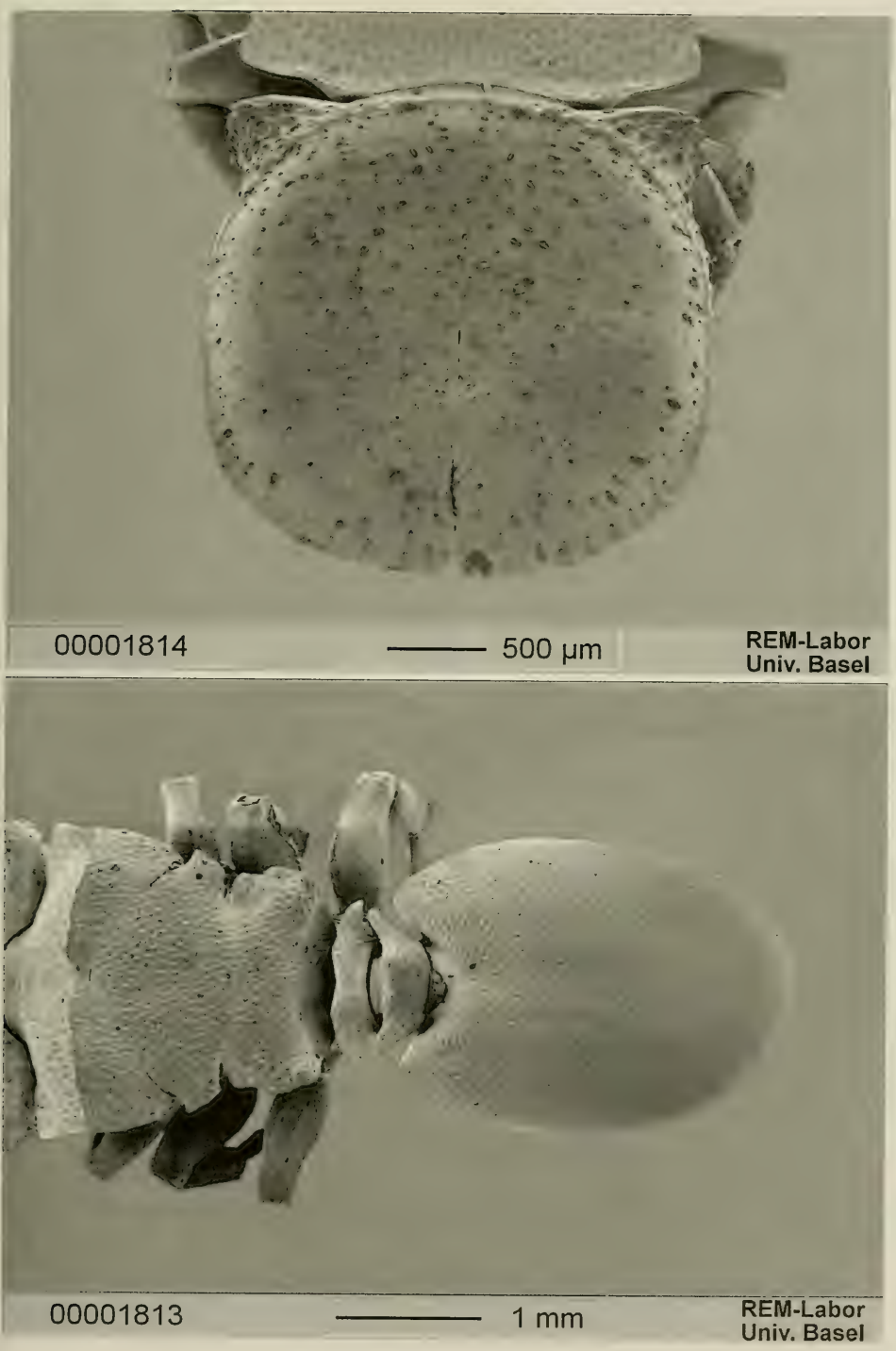


Fig. 242. *Cephalotes decolor* DE ANDRADE. Soldier from Sucre, Venezuela: head (top) and meso- and metasoma (bottom) in dorsal view.

Propodeum with differentiate basal and declivous faces; sides of the basal face with two pairs of broad, round teeth or swellings followed by a pair of stout teeth curved up and forwards.

Petiole. Anterior face truncate and slightly concave medially. Petiolar sides with a pair of broad, triangular spines. Postpetiole much more convex dorsally than in the worker; its sides with a pair of round spines directed forwards at the base.

Gaster. Oval with a pair of protruding anterior lobes.

Mid and hind femora dorsally weakly angulate and bicarinate distally.

Sculpture. Head dorsum superficially and minutely punctate and with small, sparse foveae denser on the vertex and on the vertexal angles, larger in small specimens. Floor of the disc completely shining, sometimes covered by a very thin layer of probable camouflage material. Sides of the head disc punctate, posteriorly, densely and irregularly foveolate, the foveae separate by irregular rugosities, transversal in front of the eyes, anteriorly with sparse, superficial foveae, the rugosities and the punctuations more impressed near the antennal scrobes. Ventral part of the head posteriorly shining, with superficial punctuations and sparse foveae, the punctuations more impressed and the foveae larger and denser anteriorly. Mesosoma punctate and densely foveolate. Pedicel with sculpture similar to the one of the mesosoma but the foveae shallower and smaller. Pleurae reticulate, punctate, with rugosities thin, transversal on the propleurae and longitudinal on the ventral part of the meso- and on the posterior border of the metapleurae; propleurae with additional sparse foveae. Gaster and legs sculptured as in the worker except for the sides of the first gastral tergite and sternite with less foveae.

Pilosity. As in the worker except for the much longer and denser clubbed hairs on the external border of the disc, on the sides of the head and of the vertexal angles. Cephalic disc ventrally with few clubbed hairs on the anterior border and with one layer of long, appressed hairs internally.

Colour. Dark brown to black with darker head.

Measurements (in mm) and indices: TL 6.78–8.96; HL 2.08–2.28; HW 2.00–2.32; EL 0.34–0.40; PW 1.64–2.20; PeW 0.88–1.16; PpW 0.78–1.04; HBaL 0.34–0.40; HBaW 0.16–0.19; CI 101.7–104.9; PI 104.9–105.4; PPeI 186.4–189.6; PPpI 210.2–211.5; HBaI 47.0–47.5.

G y n e . - Differing from the soldier in the following: sides of the disc with less raised border. Floor of the disc flat or gently convex medially. Vertex with a small, median, superficial concavity.

Mesosoma. Humeral angles obtuse. Pronotum, mesonotum and scutellum flat in side view. Sides of the basal face of the propodeum anteriorly convex and posteriorly with a pair of teeth slightly diverging externally.

Petiole. Anterior face oblique and separated from the posterior one by a superficial, incomplete carina. Petiolar sides with a pair of minute denticles medially. Postpetiole as in the soldier but with the lateral spines shorter and truncate.

Gaster. Similar to the one of the soldier but much longer.

Sculpture. Head dorsum superficially and minutely punctate and with dense foveae. Upper and ventral part of the lower metapleurae with dense, small foveae.

Pilosity. As in the soldier except for sides of the mesosoma with rare, long, clubbed hairs as on the sides of the head.

Colour. As in the soldier with lighter gaster and legs.

Measurements (in mm) and indices: TL 9.80–10.0; HL 2.04–2.08; HW 1.98–2.00; EL 0.43–0.45; PW 1.80–1.84; PeW 0.80–0.85; PpW 0.96–0.98; HBaL 0.51–0.52; HBaW 0.20–0.21; CI 96.1–97.0; PI 107.6–111.1; PPeI 216.5–225.0; PPpI 187.5–187.7; HBaI 39.2–40.4.

M a t e r i a l e x a m i n e d . - **Colombia**: no further locality, 29.IV.1941, 3 soldiers intercepted in Hoboken (New Jersey) [MZSP].

Venezuela: no further locality, 30.IV.1941, 1.VIII & 21.XI.1945, 5 workers, 8 soldiers, in pseudobulb of *Cattleya* intercepted in Hoboken [MZSP]; no further locality, 24.VI.1946, 3 workers in *Cattleya* sp. intercepted in San Francisco [MZSP]. L a r a : 20 km E Carora, 24.VI.1976, 2 gynes, A. S. MENKEL & D. VINCENT [USNM]. S u c r e : Parque Nacional Mochima, 50 m, 2.X.1986, 16 workers (paratypes), 4 soldiers (holotype and paratypes),

E. CANCELLO & C. R. F. BRANDÃO [MZSP]. Anzoátegui: Pto. La Cruz, 1 worker, KULZER [ZSMC].

Discussion. - The main center of variation observed among the *decolor* material seem to be the foveae on the disc of the soldiers: their size is negatively correlated with the body size. This is the largest species of the *pallens* clade.

All the specimens referred to this species had been already identified as *pallens* by KEMPF (1958 a).

Distribution: Colombia, Venezuela.

5.6.14. The *patei* clade

A small clade containing only the homonymous species *patei*. This and the following two clades (*emeryi* and *crenaticeps*) appear weakly or insufficiently defined from the results of our cladistic analysis. We could try to add additional synapomorphies for each of them or to group the three clades in one but none of these solutions (i. e. artificially constructed synapomorphies or lumping all species in a single clade) would be really convincing. *Patei* exemplifies well this situation: it bears obvious similarities with *emeryi* and *crenaticeps* for the short pronotal lamellae of the worker, and, at the same time, it remains rather distinct within the genus by the stout (not flattened) mesosoma, by the flat head, and by the very broad, spatulate hairs of the gyne and of the soldier. None of these characters are considered in our data matrix since we regard their apomorphic value as doubtful. No other apomorphies for this species result from our analysis. We did not dare dissecting the sole known male preserved in the USNM but the description of its genitalia represent the most concrete foreseeable source of information to better assess the position of this species.

Cephalotes patei (KEMPF) new combination
Fig. 243

Paracryptocerus patei KEMPF, 1951: 235, figs. 151, 153–155. Worker, soldier, gyne, male. Original description. Type locality: intercepted in New Jersey on *Cattleya* (orchids) imported from Colombia. Type material: holotype worker in the U. S. National Museum, not available for the present study; paratypes numerous workers, soldiers, gynes and one male in MZSP, MCZC and USNM (examined in part).

Zacryptocerus patei (KEMPF), BRANDÃO, 1991: 387. First combination in *Zacryptocerus*.

Diagnosis. - A distinctive species of uncertain relationships. Its most salient apomorphies are already described in the introduction to the clade.

Worker (Fig. 243) (description of KEMPF, 1951). - "Length 5.7 mm. Median head length 1.41 mm; Weber's length of thorax 1.63 mm. Black; the apex of the funicular segment and the three apical tarsal segments ferrugenous. Tips of mandibles fuscous-ferruginous.

Head subopaque, subquadrate; its maximum length distinctly shorter than the interocular width (65:72). Mandibles rugulose. Frontal carinae with semitransparent, more or less infuscated maculae; the lateral border vestigially crenulate, slightly sinuate and diverging behind, scarcely upturned above the eyes. Occipital angles obliquely truncate, the edges serrate or notched. Eyes small, their greatest diameter less than one fourth of the median head length. Upper surface of head scarcely but evenly convex, finely reticulate-punctate, more sparsely covered with squamiferous foveolae, which are somewhat denser and larger towards the occiput. Vertex without a pair of small denticules. Lower surface of head rather coarsely reticulate-rugose.

Thorax subopaque. Anterior border moderately arcuate. Shoulders subrectangular. Sides of pronotum with a flat, narrow rectangular projecting lamella, the apical border of which is

emarginate and bidentate, the posterior border emarginate and converging towards the rectangular, subdentate posterior corner of the pronotum. Promesonotal suture vestigial. Mesonotum with a small denticule on each side. Mesoepinotal suture distinct, slightly impressed. Anterior corner of basal face of epinotum rather obtuse, not sharply rectangular, the sides with a triangular tooth. Declivous face more or less differentiated from the basal face. Dorsum of thorax finely reticulate-punctate, rather densely covered with squamiferous foveolae, the slightly raised intervals between which form a coarse reticule. A few ongitudinal rugae mesad on basal face of epinotum. Declivous face of epinotum, the laterotergite of pronotum and the greater portion of the thoracic pleura coarsely longitudinally striated. Femora not angulate above at the half. Hind basitarsi compressed and somewhat broadened basad.

Peduncolar segments subopaque, the dorsolateral sculpture as on dorsum of thorax. Petiole narrower than postpetiole, its anterior face obliquely truncate, finely reticulate-punctate, subfulgid, without macrosculpture and pilosity. Anterior corners subangulate, the sides with a small, acute tooth. Postpetiole with a slender, acute tooth, arising from the anterior corner. Upper face flat, not bordered by longitudinal ridges.

Gaster short, suboval, subopaque. Strongly convex above. Scarcely emarginate in front mesad, the anterolateral border sharply marginate and crested. Length: depth proportion less than 1.5 (75:55). First gastral tergite finely reticulate-punctate, more coarsely areolate-rugose, each areole containing a shallow squamiferous groove. Sculpture not evanescent discally.

Sides of head, excluding truncate occipital angles, sparsely beset with short, whitish, thick, projecting setulae, which are somewhat longer than those of *emeryi*. Upper surface of head, thorax, peduncle and gaster with oval, canaliculate scales, shorter than those of *emeryi* and not as aureate. Strictly silvery on the appendages and the densely scaled areas of the thoracic pleura. Apical borders of gastral tergites and sternites with common, sparse, erect pile."

Measurements (in mm) and indices: TL 5.40–5.72; HL 1.34–1.36; HW 1.68–1.72; EL 0.36; PW 1.52–1.60; PeW 0.56–0.64; PpW 0.68–0.72; HBaL 0.60–0.64; HBaW 0.22; CI 125.4–126.5; PI 105.0–113.1; PPeI 237.5–285.7; PPpI 222.2–235.3; HBaI 34.4–36.7.

S o l d i e r (description of KEMPF, 1951). - "Length 7.3 mm. Median head length 1.97 mm; Weber's length of thorax 2.10 mm. Black; the frontal carinae dark rufous brown; tip of last funicular segment and three apical tarsal segments ferruginous.

Head subopaque; surmounted by a circular, flat, completely marginate disc, with an antero-median emargination, exposing the strongly rugose mandibles from above. Anterolateral border of disc crenulate, the median portion of the posterior border strictly truncate, forming a bidentate crest above the perpendicularly truncate occiput. Floor of disc very slightly raised in the middle, just behind the vestigially outlined clypeus, and again less prominently farther behind on the vertex, very shallowly excavate laterad of the anterior convexity where the margins are slightly upturned. Occipital angles blunt, rounded, carinulate. Eyes moderately convex. Lower border of cheeks carinate. Upper surface and sides of head finely reticulate-punctate, coarsely, densely and deeply foveolate. Lower surface of head fulgid, areolate-foveolate.

Thorax subopaque. Shoulder angle scarcely visible from above. Pronotum greatly expanded on each side, the anterior angle acute and subdentate, the posterior angle bluntly rounded. Transverse pronotal crest strong and greatly raised, narrowly interrupted in the middle by a cut-like longitudinal incision. Promesonotal suture distinct. Sides of mesonotum bluntly rounded, the posterior border bisinuate, followed by a deeply impressed metanotal groove. Basal face of epinotum conspicuously transversely convex, with a short broad tooth on the sides and another similar tooth on the posterior corners. Declivous face more than twice as long as the basal face, immarginate laterad. Sculpture as on upper surface of head, the squamiferous foveolae more crowded and smaller. Sides of the thorax coarsely rugose. Legs as in worker. Peduncular segments and gaster similar to those of the worker; the postpetiole and petiole narrower.

Rim of projecting setulae extending around the disc to the posterior border of the eyes. Scales within the foveolae oval, canaliculate, as in worker."

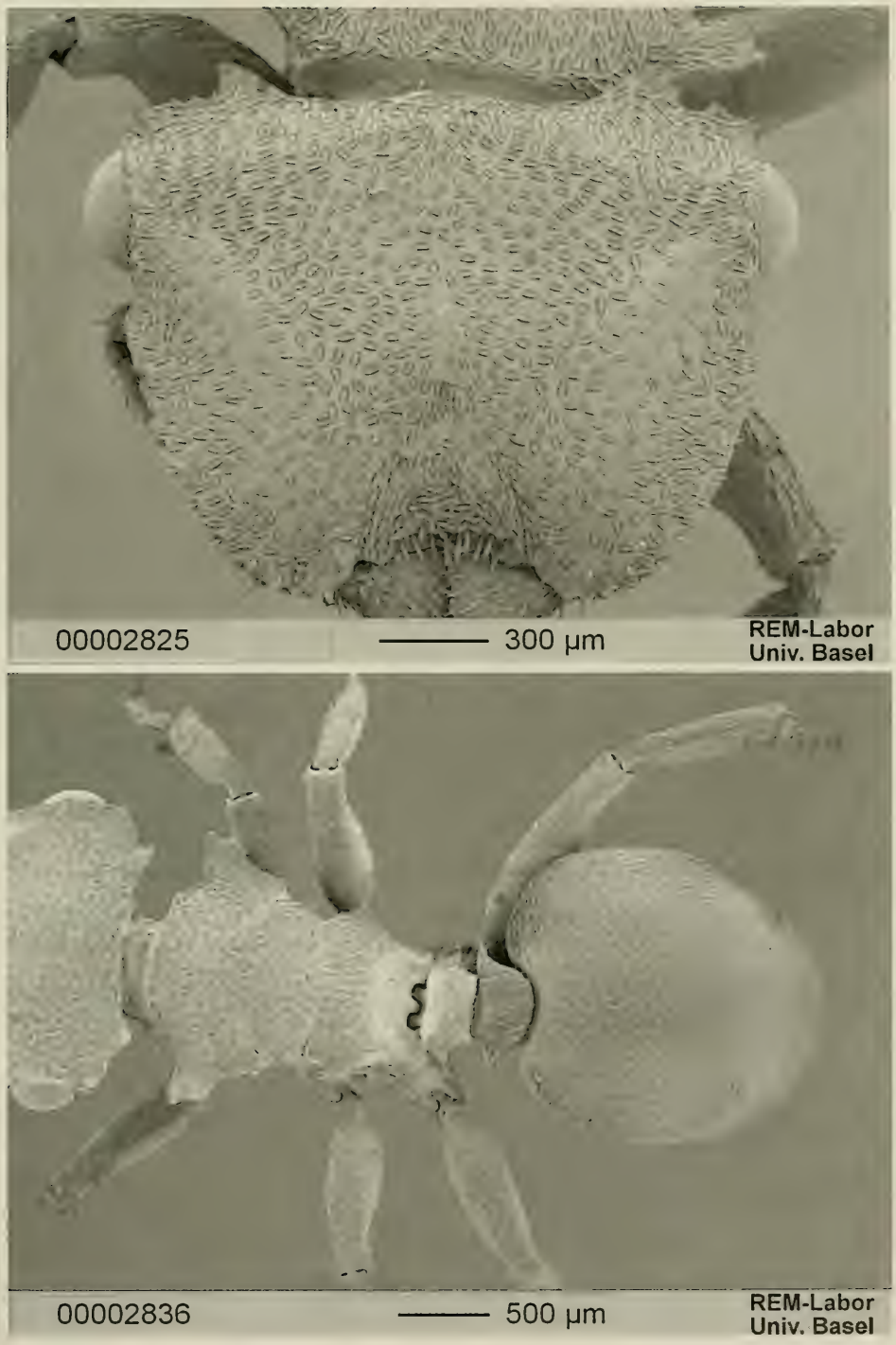


Fig. 243. *Cephalotes patei* (KEMPF). Worker from Colombia (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Measurements (in mm) and indices: TL 7.60–7.72; HL 2.00; HW 2.32; EL 0.40; PW 2.20–2.28; PeW 0.72–0.76; PpW 0.76–0.80; HBaL 0.72; HBaW 0.26; CI 116.0; PI 101.7–105.5; PPeI 300.0-305.5; PPpI 285.0–289.5; HBaI 36.1.

G y n e (description of KEMPF, 1951). - "Length 8.2 mm. Median head length 1.97 mm; Weber's length of thorax 2.39 mm. Resembling the soldier in color, sculpture pilosity and general structure, with the exception of the peculiarities of the caste and the following details:

Head disc still flatter, the postero-lateral border only faintly marginate, the posterior portion behind the deeply sunken ocelli slightly curved downwards. The posterior border crested as in the soldier. Shoulders obsolete. Transverse pronotal crest distinct, not as strong nor as highly raised as in the soldier, the median interruption broader, not slit-like. The anterior tip of the lateral expansion of the pronotum forming an acute large, triangular tooth. Scutellum longitudinally convex. Basal face of epinotum very short, the lateral and posterior teeth more obtuse. Lower mesopleura with a strong tooth. First gastral tergite longer than the maximum length of the thorax (118:98). Gaster somewhat longer than in soldier. Wings hyaline, the veins brunneus, the stigma fuscous. Fore wing with a closed and appendiculate marginal cell and a transverse cubital vein. The second abscissa of the median vein not much longer than the transverse median vein."

Measurements (in mm) and indices: TL 8.96–9.12; HL 2.00–2.04; HW 2.24–2.30; EL 0.41; PW 2.12–2.16; PeW 0.68; PpW 0.77–0.79; HBaL 0.76; HBaW 0.29; CI 112.0–112.7; PI 108.5–1.08.7; PPeI 331.8-317.6; PPpI 269.3–280.5; HBaI 38.1.

M a l e (not seen for the present study; description of KEMPF, 1951). - "Length 6.4 mm. Median head length 0.9 mm; Weber's length of thorax 2.19 mm. Black; the tip of mandibles, antennae, legs and gaster brunneous.

Head subopaque; transverse. Distance between the eyes longer than the median head length (49:39). Mandibles finely and densely punctate, somewhat rugulose at apex. Chewing border with a strong apical and postapical tooth, and three following minute teeth. Clypeus convex, with a transverse incision, near the posterior border. Front slightly impressed in front of the anterior ocellus. Eyes large, their maximum diameter slightly less than half of the median head length (18:39). Ocelli raised on short sockets. A vestigial crest extending from behind the eye to the bluntly rounded, yet visible occipital angle. Integument finely reticulate-punctate and rugose, the rugae being transverse between the eyes and the rather smooth front, forming a network between the cheeks, the occiput and the lower surface of the head. Scape and first antennal segment glabrous. Length of scape about one half of the second funicular segment.

Thorax subopaque, somewhat similar to that of the female. Pronotum with similarly projecting anterolateral, apically pointed, lobes on each side. Transverse crest inconspicuous, obsolescent towards the sides, ininterrupted mesad. Mayrian furrows deeply impressed in scutum. Epinotum unarmed. Sculpture as on head. The posterior portion of the sides and the epinotum with highly raised, undulating ridges, longitudinal on the sides, more or less transverse on the basal face of the epinotum.

Petiole about as long as wide, anterior face obliquely truncate, sides unarmed. Dorsal and lateral face covered with a network of raised ridges. Postpetiole slightly broader than petiole, with a tubercular tooth on each side, somewhat in front of the half. Sculpture as on petiole, ridges less conspicuous and predominantly longitudinal in direction.

Gaster subfulgid, very finely reticulate. First gastral tergite without erect pile. Head and thorax with abundant, long, flexuose, whitish and erect pile. A thin brush of similar hairs arising from beneath the postpetiole. Setae shorter, stiffer sparser and suberect on the remaining tergites of the gaster and on the sternites. Legs with similar pile, which is sparse and subdecumbent.

Wings short, scarcely projecting beyond the tip of the gaster when folded, hyaline, the veins pale brunneous, the stigma darker. Venation similar to that of female. Second abscissa of median vein subequal in length to the transverse median vein."

M a t e r i a l e x a m i n e d. **United States** (all interceptions in plant quarantine stations): N e w J e r s e y: 16.V.1946, Hoboken, no. 46–8292, 1 worker (paratype)

[MCZC]; 04.X.1946, Hoboken, no. 46–8631, on *Cattleya* sp., 3 workers, 2 soldiers (paratypes) [MZSP], all on orchids imported from Colombia; California: 01.VII.1938, 17–18.I.1940, San Francisco, 2 workers, 2 soldiers, 2 gynes [MZSP].

Discussion. - A poorly known species which had been never collected in its natural environment. All the U. S. records are interceptions in plant quarantine stations. It is separable at glance from the members of its closest clades by the lack of vertexal denticles and, in particular, from *crenaticeps* and *ecuadorialis* by the lack of coloured spots on the gaster of all three female castes and from *emeryi* by the coloration, brown with lighter frontal carinae instead of uniformly black.

Distribution: Colombia? (known only from samples of probable Colombian origin intercepted at U. S. plant quarantine stations).

5.6.15. The *emeryi* clade

This clade contains two Dominican fossil species and a Recent one from Curaçao. The exact relationships among the three and with other *Cephalotes* species may be subject to future changes since all of them are known on workers only. Its members are unique within a large, terminal *Cephalotes* clade comprising 52 species, for the secondary loss of the coloration of the frontal carinae. This character is likely to have an obvious adaptive and a doubtful phylogenetic meaning. See also the introduction to the *patei* clade.

Species included in the clade: *emeryi*, *jansei*, *serratus*.

Cephalotes emeryi (Forel) new combination

Cryptocerus emeryi Forel, 1912: 203. Worker. Original description. Type locality: Curaçao. Type material: lectotype worker designated by Kempf, 1951 and two syntype workers from Curaçao (Landolt) in MHNG, examined.

Paracryptocerus emeryi (Forel), Kempf, 1951: 233, figs. 156, 157. Worker. First combination in *Paracryptocerus*.

Zacryptocerus emeryi (Forel), Brandão, 1991: 386. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *emeryi* clade differing from the other two species of the clade by the absence of long, flexuous hairs.

Worker (description of Kempf, 1951). - "Length 5.3 mm. Median head length 1.24 mm; Weber's length of thorax 1.51 mm. Black; tip of last funicular segment and apical tarsal segments dark ferruginous. Tips of mandibles rufous-brown.

Head subopaque, subquadrate; its maximum length slightly longer than the interocular width (61:58). Mandibles rugulose. Frontal carinae not transparent nor membranous, their lateral border vestigially crenulate in front, slightly diverging behind, sinuate, scarcely upturned above the eyes. Occipital angles obliquely truncate, not serrated nor notched. Eyes small, greatly convex, their greatest diameter less than 1/4 of the median head length. Upper surface of head somewhat convex discad, flatter towards the sides, finely reticulate-punctate, sparsely covered with squamiferous foveolae, which are slightly denser and encircled by a raised network of rugae towards the sides and the occiput. Vertex with a more or less vestigial pair of small denticles.

Thorax subopaque. Anterior border moderately arcuate. Shoulders angulate. Sides of pronotum with a flat, narrow, rectangular projecting lamella, the posterior border of which is emarginate and converges obliquely toward the posterior, rectangular corner of the pronotum. Promesonotal suture vestigial. Mesonotum with a faint denticle on each side. Mesoepinotal suture deeply impressed laterad, obsolescent mesad. Anterior corner of basal face of epinotum sharply rectangular, the sides with a strongly projecting rectangular tooth.

Declivous face more or less differentiated from the basal face. Dorsum of thorax finely reticulate-punctate, coarsely areolate-rugose, each areole containing a squamiferous foveola. Basal face of epinotum longitudinally striato-rugose. Declivous face without distinct macrosculpture and pilosity. Sides of thorax rather coarsely and more or less longitudinally rugose. Femora not angulate above at half. Hind basitarsus little compressed and broadened.

Peduncular segments subopaque, dorso-lateral sculpture as on dorsum of thorax. Petiole narrower than the postpetiole, its anterior face obliquely truncate, finely reticulate-punctate, without macrosculpture nor pilosity. Anterior corners rounded, the sides with a small tooth, constricted and converging behind the tooth. Postpetiole with a stout, thick, lateral, triangular tooth, arising from the anterior corner, pointing obliquely backwards and sidewards. Dorsal face with a pair of vestigial longitudinal ridges.

Gaster short, elliptical, subopaque, slightly emarginate in front mesad, not extremely convex above, the length: depth proportion being more than 1.5 (69:43). The anterolateral border sharply marginate, not crested. First gastral tergite finely reticulate-punctate, longitudinally rugulose. Sculpture evanescent discally, where the integument is almost smooth and subfulgid.

Sides of head, including the truncate occipital corners, sparsely beset with short, thick, whitish, projecting setulae. Upper surface of head, thorax, peduncle, and gaster with long, flat, decumbent, light, aureate, scale-like hairs, which are longitudinally canaliculate. Scales very dense on the basal face of the epinotum and the peripheral portions of the first gastral tergite. Scales sparser on the sides of the thorax. Small and sparse on the appendages."

Measurements (in mm) and indices: TL 5.20–5.78; HL 1.24–1.36; HW 1.44–1.58; EL 0.32–0.34; PW 1.32–1.48; PeW 0.51–0.63; PpW 0.55–0.62; HBaL 0.49–0.52; HBaW 0.15–0.16; CI 116.1–116.2; PI 106.7–109.1; PPeI 234.9–258.8; PPpI 238.7–240.0; HBaI 30.6–30.8.

Material examined. - **Curaçao**: no further data, lectotype worker, 2 syntype workers, LANDOLT [MHNG].

Discussion. - This species is very close to both Dominican fossils *jansei* and *serratus* and it is particularly interesting the fact that it appears to be endemic of another Antillean island. There is, however, the possibility that this similarity may be in part spurious and resulting from the fact that the three species are known only on workers.

Distribution: Curaçao.

† *Cephalotes serratus* (VIERBERGEN & SCHEVEN) new combination
Figs. 3–6, 17 A, B, 244, 245

Zacryptocerus sp., BARONI URBANI & SAUNDERS, 1980: 221, pl. 2, fig. 2. Worker.
Zacryptocerus sp., JASTRZEBSKI, 1985: 1, fig. 1. Worker.
- ANONYMOUS, 1990: cover page figure. Worker.
Exocryptocerus serratus VIERBERGEN & SCHEVEN, 1995: 159, figs. 1 a-c. Worker. Dominican amber. Original description. Type material: holotype in the JSHC, examined, two paratypes in MCZC (our reference numbers MCZC–2 and MCZC–11), examined.
Exocryptocerus elevatus VIERBERGEN & SCHEVEN, 1995: 160, figs. 2 a-d. Worker. Dominican amber. Original description. Type material: holotype (unique) in the JSHC, examined. New synonym.
Exocryptocerus truncatus VIERBERGEN & SCHEVEN, 1995: 161, figs. 3 a-d. Worker. Dominican amber. Original description. Type material: holotype (unique) in the JSHC, examined. New synonym.

Diagnosis. - A member of the *emeryi* clade characterised, in the worker, by the long, flexuous hairs and by the HBaI $\geq$ 40.0.

Worker (Figs. 244, 245). - Head subquadrate. Frontal carinae sparsely and variably crenulate, not upturned above the eyes. Vertexal angles with a round or truncate lamella with

crenulate border. Vertexal margin concave. Vertex with a pair of small denticles. Mandibles laterally angulate.

Mesosoma. Scapular angles present in some specimens only. Anterior pronotal border straight, protruding anteriorly and passing into the sides with a long, weak concavity. Pronotal sides with a pair of broad, continuos lamella or with a pair of broad, obtuse teeth converging backwards. Promesonotal suture superficially marked or invisible. Propodeal suture marked. Sides of the mesonotum straight or with a pair of round or truncate teeth. Propodeum with differentiate basal and declivous faces; sides of the basal face marked anteriorly and posteriorly by an angle; declivous face of the propodeum converging posteriorly. Some specimens with the whole mesosomal border slightly crenulate.

Petiole. Anterior face truncate, posterior face slightly concave medially. Petiolar sides with a pair of minute denticles or small teeth. Postpetiolar node superficially concave in the middle; anterior half of the postpetiolar sides with a pair of round, variably broad, teeth directed laterally.

Gaster suboval, with a pair of variably developed anterolateral lamellae or with small lobes.

Fore coxae angulate. Mid and hind femora without angle or denticles. Mid and hind basitarsi flattened and with broad base.

Sculpture. Head dorsum minutely punctate and covered with foveae variably clumped. Ventral face of the head superficially punctate-foveolate with superimposed irregular, longitudinal rugosities. Mesosoma minutely punctate and with dense, slightly irregular, foveae; this sculpture on the propodeum is superimposed to longitudinal, irregular rugosites. Peduncular segments with the same type of sculpture as on the propodeum but more superficial. Gaster reticulate; the reticulation more superficial on the center of the first gastral sternite. Legs strongly reticulate and with few, superficial, longitudinal rugosities.

Pilosity. Each fovea with a thin, pointed, flexuous hair of variable size; similar hairs but denser on the legs, on the gaster, and on the crenulation of the frontal carinae.

Colour. Some specimens have frontal carinae, vertexal angles, pronotal sides and gastral lamellae ferruginous and semitransparent while, in others, these parts are completely black.

Measurements (in mm) and indices: TL 3.82–6.00; HL 0.961.36; HW 1.24–1.60; EL 0.24–0.28; PW 1.12–1.48; PeW 0.50; PpW 0.40–0.60; HBaL 0.42–0.56; HBaW 0.16–0.22; CI 123.1–129.2; PI 108.1–118.5; PPeI 246.7-306.4; PPpI 217.6-308.3; HBaI 40.0–42.3.

Material examined. - **Dominican amber**: 21 workers in the SMNS (reference numbers: Do-333-K, Do–551, Do–974-K, Do–1069-K 1 & 2, Do–1069, Do–2457, Do–2622, Do–2806, Do-3224, Do-3274, Do-3487, Do-3862, Do-3980, Do–4210, Do–4214, Do–4480, Do–4962-A, Do–5163, Do–5226, Do–5492); 4 workers in the GOPC (reference numbers: H 10–116 B, H 10–116 D, H 10–116 E, H 10–116 I); 3 workers in the JSHC (holotype of *serratus*; holotype of *elevatus*; holotype of *truncatus*); 5 workers in the MCZC (our reference numbers MCZC–2, MCZC–11 from the mine La Toca, both paratypes of *serratus*, MCZC–8, MCZC–13, MCZC-16 from the mine La Toca; 3 workers from NHMB (reference numbers: PE 112, PE 113, PE 114).

Discussion. - We have already shown in Chapter 5 that the genus *Exocryptocerus* in which *serratus* was originally described has no reason to exist. *C. serratus* is the sister species of *jansei* and both species are distinguishable by the shape of the pronotal lamellae and by the different values of HBaI as already given in their relative diagnoses and descriptions.

The numerous specimens we refer to *C. serratus* show remarkable variation in body shape and sculpture. This variability affects the following characters: 1. The shape of the pronotal lamellae which can be continuous or with a pair of broad, triangular teeth narrowing posteriorly. 2. The foveae on the head can be dense or sparse. 3. The body pilosity which can be dense or sparse. 4. The sides of the propodeum, with two angles or with two small denticles. 5. The gastral lamellae,

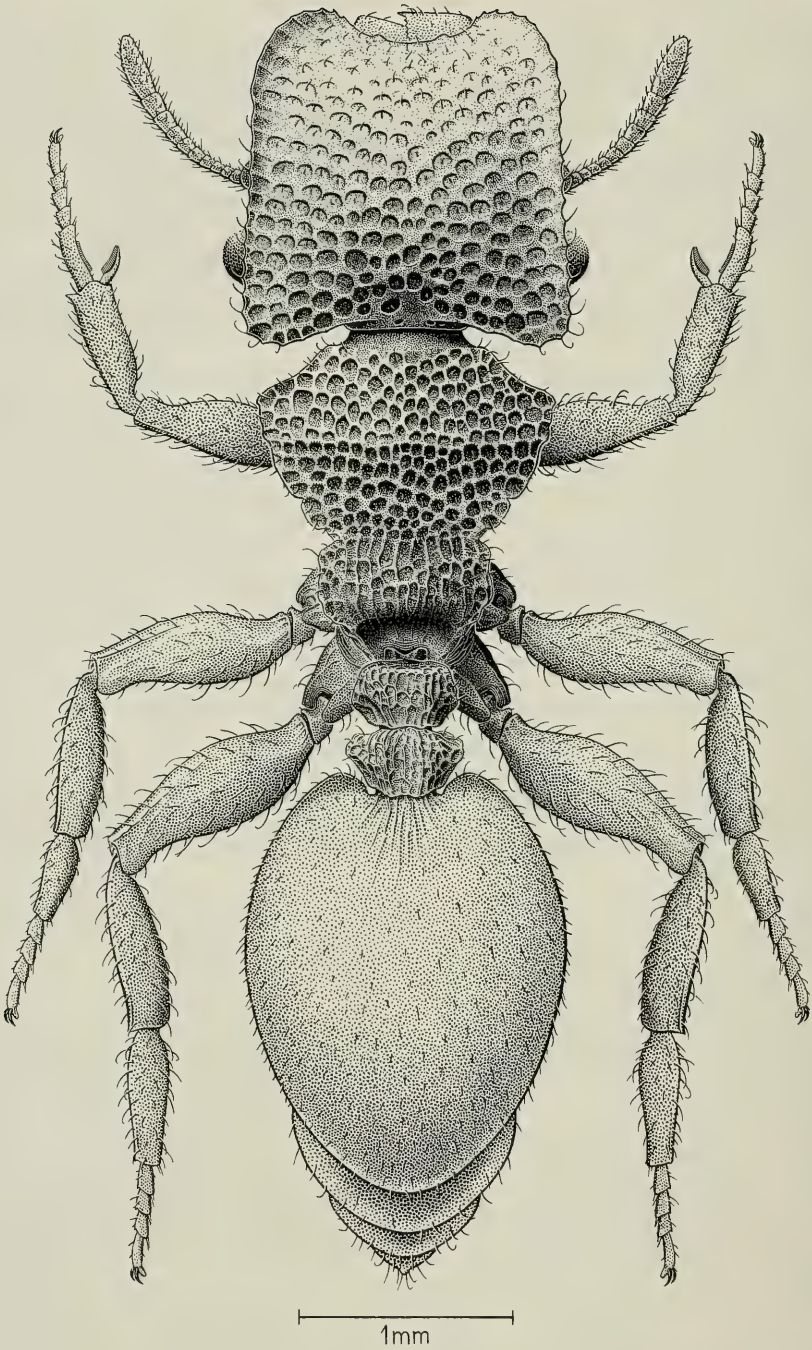


Fig. 244. *Cephalotes serratus* (VIERBERGEN & SCHEVEN) from Dominican amber. Worker in dorsal view.

Fig. 245. *Cephalotes serratus* (VIERBERGEN & SCHEVEN) from Dominican amber. Worker mesosoma exemplifying another possible morphology. Transitional forms between the morphology illustrated here and that of Fig. 244 are frequent.

differently developed in different specimens. 6. The width of the peduncular segments.

We have been unable to trace one single, credible, specific boundary within the 36 specimens we refer to this species. The comparison of single pairs of individuals, of course, may reveal remarkable differences. Lack of sufficient material to appreciate this variability may explain the descriptions of *elevatus* and of *truncatus* (based on one specimen each). The holotypes of *truncatus* and *elevatus* represent simply large workers of *serratus* as suggested by the fact that these specimens possess a trace of pronotal carina more evident in *elevatus*. The SMNS sample Do–4210 contains 4 large workers, all larger than the holotype of *elevatus*. Three specimens in this same sample (Do–4210) possess thin, complete, pronotal carinae and the vertex with a transversal, short carina.

The synonymy of both *elevatus* and *truncatus* with *serratus* appears unavoidable according to our interpretation of *serratus* as a single, variable species. *Serratus* is, together with *squamosus*, one of the two most common and most variable *Cephalotes* amber species. We explain the correlation between frequency and variability with the probably wider age range from which the specimens have been sampled. See also the discussion under *C. squamosus*.

The amber from La Toca where part of these specimens have been collected is estimated to be 30–45 Ma old (POINAR, 1992).

D i s t r i b u t i o n : Dominican amber.

† *Cephalotes jansei* (VIERBERGEN & SCHEVEN) new combination
Figs. 11 A, B, C, 246

Exocryptocerus jansei VIERBERGEN & SCHEVEN, 1995: 161, figs. 4 a-d. Worker. Dominican amber. Original description. Type material: holotype worker in the JSHC, examined; paratype worker in MCZC, reference number MCZC–4, examined.

D i a g n o s i s . - A member of the *emeryi* clade characterised, in the worker, by the long, flexuous hairs, by the pronotal sides with a broad, pointed triangular tooth and by HBaI < 35.0.

W o r k e r (Fig. 246). - Head subquadrate. Frontal carinae strongly but sparsely crenulate, not upturned above the eyes. Vertexal angles with a truncate, crenulate lamella. Vertexal margin concave. Vertex with a small pair of denticles. Mandibles laterally angulate.

Mesosoma. Scapular angles present. Anterior pronotal border straight. Pronotal sides with a broad, pointed, triangular teeth. Promesonotal suture marked. Sides of the mesonotum straight and with a pair of posterior angles. Propodeum with differentiate basal and declivous faces; sides of the basal face marked anteriorly and posteriorly by an angle; sides of the declivous face converging posteriorly.

Petiole. Anterior face truncate, posterior face gently concave medially; petiolar sides with a pair of minute denticles. Postpetiolar node also weakly concave in the middle; anterior half of the postpetiolar sides with a pair of round, broad teeth arising from the anterior border of the postpetiole and directed laterally.

Gaster suboval, with a minute pair of anterior lobes.

Fore coxae angulate. Mid and hind femora without angle or denticles. Mid and hind basitarsi flat and with slightly broad base.

Sculpture. Head and mesosoma minutely punctate and with superimposed dense, irregular foveae; this sculpture on the posterior half of the mesonotum and on the anterior part of the propodeum is superimposed to irregular, longitudinal rugosites. Peduncular segments with the same sculpture as on the head dorsum but with smaller foveae. Frontal carinae with the same type of sculpture as on the head dorsum but more superficial. Ventral face of the head punctate and with irregular, superficial foveae and rugosities. Gastral tergites and sternites reticulate; the reticulation more superficial on the center of the first gastral sternite. Legs strongly reticulate and with superimposed irregular, faint rugosities.

Pilosity. Each fovea with a long, thin, pointed, flexuous hair; hairs similar or longer but denser on the legs and on the gaster and on the crenulation of the frontal carinae.

Colour. Ferruginous.

Measurements (in mm) and indices: TL 4.69–5.48; HL 1.22–1.32; HW 1.50–1.77; EL 0.27–0.30; PW 1.48–1.52; PeW 0.50; PpW 0.52–0.60; HBaL 0.52–0.63; HBaW 0.16–0.22; CI 122.9–134.1; PI 101.3–116.4; PPeI 296.0-304.0; PPpI 246.7–292.3; HBaI 30.8–34.9.

M a t e r i a l e x a m i n e d . - **Dominican amber**: 1 worker (holotype) in the JSHC; 1 worker (paratype) in the MCZC (reference number MCZC–4); 1 worker in the GOPC (reference number: H 10–121).

D i s c u s s i o n . - We already showed in chapter 5 that the genus *Exocryptocerus* in which *jansei* was originally described is unjustified. *C. jansei* is the sister species of *C. serratus* and both are easily differentiated within the *emeryi* clade by the flexuous body hairs. *C. jansei* is very similar to *serratus* but it has the pronotal lamellae with a pair of broad, triangular teeth, the gaster with short anterolateral lobes and HBaI < 35.0.

The specimen H 10–121 (on which our drawing is based) differs from the holotype for having denser body hairs and sparser foveae on the head. Since we observed analogous pilosity and sculpturation variability in other fossil species, like *serratus* and *squamosus*, we think it appropriate to consider the specimen H 10–121 as *jansei* in spite of these differences.

D i s t r i b u t i o n : Dominican amber.

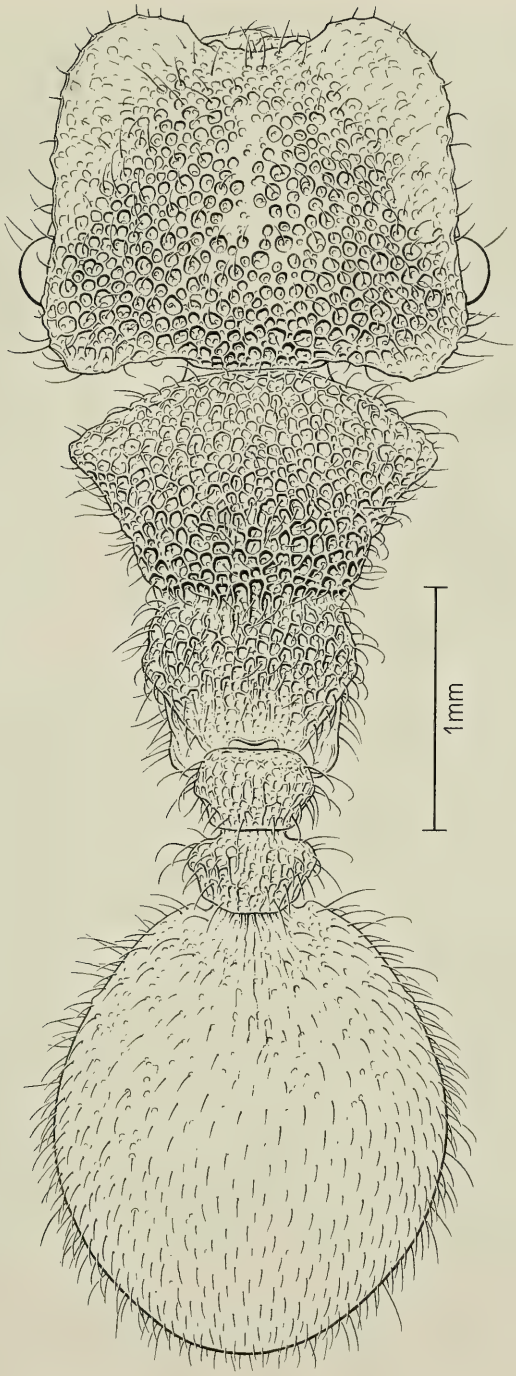


Fig. 246. *Cephalotes jansei* (VIERBERGEN & SCHEVEN) from Dominican amber. Worker in dorsal view. Appendages omitted.

5.6.16. The *crenaticeps* clade

This small clade (only two species), like the previous two clades, possess no known strong synapomorphies. The sole character resulting uniquely shared by descent among its two members and resulting from our analysis are the propodeal spines of the gyne, diverging backwards. This character is rare but not unique within *Cephalotes* and we are rather sceptic about its phylogenetic importance. See also the introduction to the *patei* clade. To increase the insecurity about the distinction between this clade and the *emeryi* clade, one could add that *crenaticeps* and *emeryi* (belonging to the *emeryi* clade) are rather similar in pilosity and for having the gaster anteriorly without lobes.

Species included in the clade: *crenaticeps*, *ecuadorialis*.

Cephalotes crenaticeps (MAYR) new combination
Figs. 247, 248, 249, 250

Cryptocerus crenaticeps MAYR, 1866 a: 515. Gyne. Original description. Type locality: Colombia. Type material: holotype gyne labelled "Columb., Typ., Collect. G. Mayr, *crenaticeps* G. Mayr, Type" in NHMW, examined.

Paracryptocerus crenaticeps (MAYR), KEMPF, 1958 a: 138. First combination in *Paracryptocerus*.

Zacryptocerus crenaticeps (MAYR), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *crenaticeps* clade differing from its sister species, *ecuadorialis*, by the absence of gastral expansions.

W o r k e r (Fig. 247) (previously undescribed). - Head subquadrate. Frons convex. Frontal carinae crenulate, little upturned above the eyes. Vertexal angles truncate, bearing a narrow, membranaceous expansion with strongly crenulate margin. Vertexal margin concave. Vertex with a pair of minute denticles better marked in larger specimens. Mandibles with a lateral carina.

Mesosoma. Scapular angles free. Anterior pronotal border gently convex. Pronotal sides with a pair of triangular, pointed, semi-membranaceous teeth and converging posteriorly in an obtuse, short tooth. Promesonotal suture in dorsal view better impressed on the sides. Propodeal suture impressed. Mesonotum with or without a minute pair of denticles. Propodeum with a small swelling or denticle between the basal and declivous faces; sides of the basal face straight; sides of the declivous face converging posteriorly.

Petiole with truncate anterior face, gently sloping anteriorly and with a small pair of minute denticles dorsally; posterior face flat. Petiolar sides diverging into a small denticle medially and strongly converging posteriorly. Postpetiolar node gently concave dorsally; postpetiolar spines directed slightly forwards at the base and curved backwards at the apex.

Gaster. Suboval without protruding lobes or membranaceous expansions.

Hind femora without angles or denticles. Hind basitarsi long, flat and slightly broader at the base.

Sculpture. Head dorsum, mesosoma and pedicel reticulate and covered by oval foveae broader then their interspaces, the foveae slightly denser on the vertexal angles and mesosoma, smaller and superficial on the pedicel, and larger and less regular on the ventral part of the head. Frontal carinae reticulate and with sparse and superficial foveae. Declivous face of the propodeum and propleurae longitudinally rugulose and with rare, superficial foveae on the propleurae only. Meso- and metapleurae reticulate and superficially foveolate. Gaster strongly reticulate and with superficial, minute foveae. Anterior third of the first gastral sternite and sides of the remaining two thirds covered with thin, longitudinal, posteriorly concentric rugosities. Legs with the same sculpture as the gaster but with the foveae more impressed on the extensor face of femora and tibiae.

Pilosity. As in *ecuadorialis*.

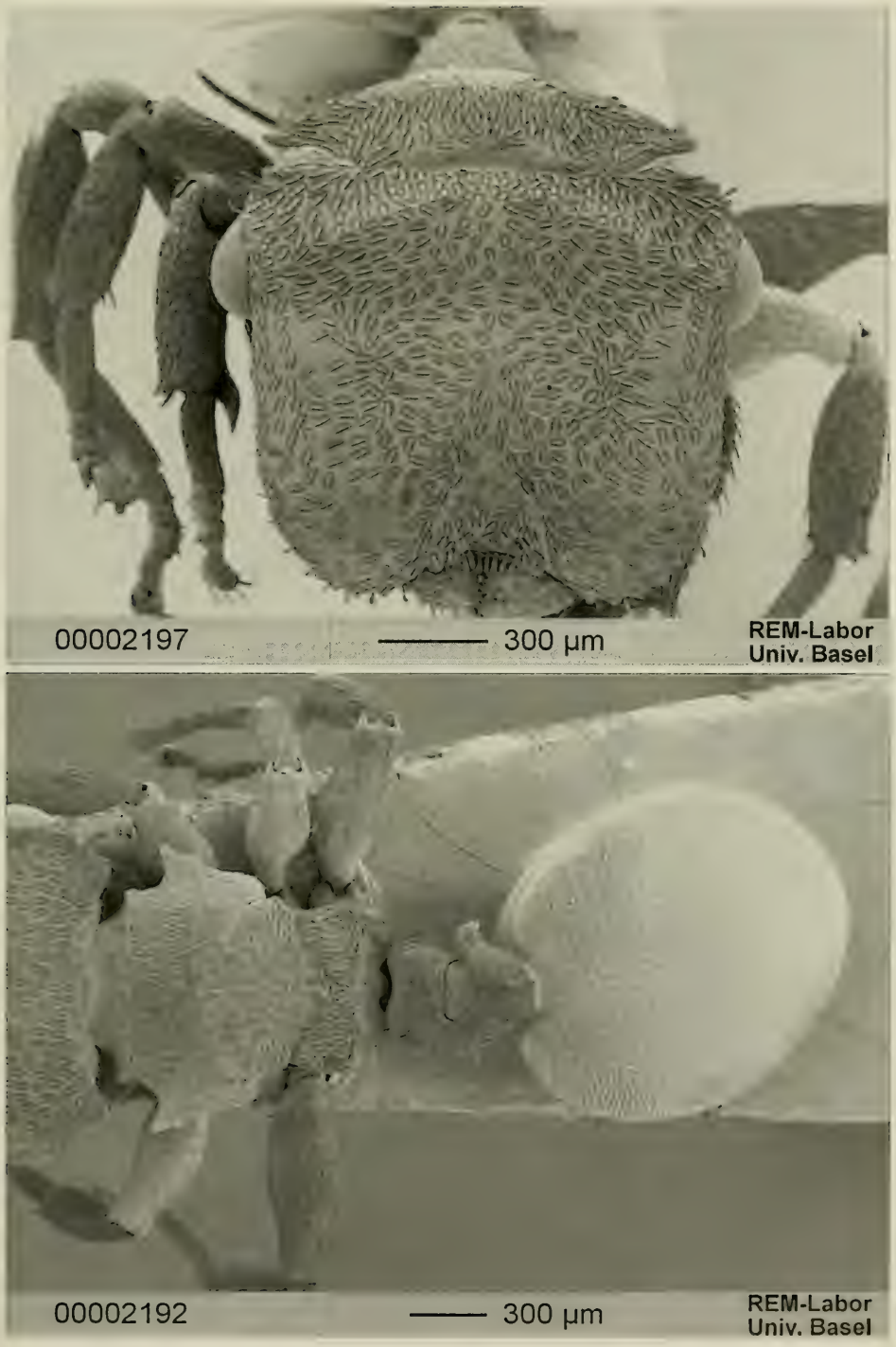


Fig. 247. *Cephalotes crenaticeps* (MAYR). Worker from Venezuela (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Colour. Dark brown. Frontal carinae yellowish to light brown and semi-transparent. Membranaceous expansion of the vertexal angles, tip of the pronotal teeth and of the postpetiolar spines light brown. First gastral tergite with a pair of oval, anterolateral, orange spots shortly surpassing the stigma posteriorly. Proximal half of the femora light brown, distal half of the femora and remaining legs yellowish to ferruginous.

Measurements (in mm) and indices: TL 4.00–4.40; HL 100–1.06; HW 1.12–1.20; EL 0.26–0.28; PW 0.95–1.08; PeW 0.47–0.48; PpW 0.54–0.56; HBaL 0.41–0.44; HBaW 0.10–0.11; CI 112.0–113.7; PI 111.1–117.9; PPeI 202.2–225.0; PPpI 175.9–192.8; HBaI 24.4–25.0.

S o l d i e r (Fig. 248) (previously undescribed). - Head disc subquadrate, with strongly crenulate border and much more raised on the sides than posteriorly; sides of the disc broad anteriorly, not covering completely the eyes and strongly converging after the eyes to a short, straight carina on the vertex. Floor of the disc with a small medial tumulus. Vertexal angles obtuse to pointed, completely separate from the disc and with strongly crenulate border. Mandibles laterally carinate and laterally hidden by the frontal carinae.

Mesosoma. Anterior pronotal border straight. Scapular angles free. Humeral angles diverging to a broad, triangular, pointed spine where they continue into the pronotal crest. Poste-rior half of the pronotal sides strongly converging. Pronotal carina high, superficially crenulate and diminishing in height only in the middle where it is notched. Pronotal suture variably impressed. Promesonotal suture deeply impressed. Mesonotal sides with a small pair of broad, round or apically pointed teeth. Propodeum with differentiate basal and declivous faces; sides of the basal face with two pairs of teeth, the first pair in the middle, the second pair between the two faces and curved upwards. Declivous face of the propodeum narrowing posteriorly.

Petiole and legs as in the worker.

Gaster oval, little protruding anterolaterally and with a faint margin not surpassing the stigma posteriorly.

Sculpture. Head dorsum superficially reticulate and covered with round foveae broader than their interspaces. Ventral face of the head reticulate and with broad, dense, deep, oval foveae forming few, irregular rugosities. Mesosoma and pedicel reticulate and covered by oval foveae, larger on the pronotum, denser and smaller on the mesonotum and propodeum, superficial on the pedicel. Declivous face of the propodeum reticulate only. Pleurae reticulate and with oval foveae, sparser on the propleurae. Propleurae with few, irregular rugae. Gaster reticulate and with minute, superficial foveae. Legs with the same sculpture as on the gaster but with the foveae better impressed on the extensor face of the femora and tibiae. Anterior third of the first gastral sternite and sides of the two posterior thirds with thin, irregular rugosities. Middle of the first sternite shining.

Pilosity. Each fovea with an appressed, broad hair. Sides of the frontal carinae, of the vertexal angles, of the mesosoma, of the pedicel and first gastral tergite with clubbed hairs. Similar hairs or slightly longer on the border of the remaining gastral segments and on the legs. First gastral sternite and border of the remaining ones with sparse, long, pointed hairs.

Colour. Dark brown. Frontal carinae, border of the vertexal angles, of the pronotal and postpetiolar spines reddish. First gastral tergite anterolaterally with a pair of oval, orange spots shortly surpassing the stigma posteriorly. Proxima half of he femora light brown, distal half and remaining legs yellowish to ferruginous.

Measurements (in mm) and indices: TL 6.04; HL 152–1.56; HW 1.68–1.72; EL 0.30; PW 1.74–1.80; PeW 0.62; PpW 0.69–0.72; HBaL 0.48–0.50; HBaW 0.14; CI 107.7–113.1; PI 93.3–98.8; PPeI 280.6–290.3; PPpI 250.0–252.2; HBaI 28.0–29.2.

G y n e (Fig. 249). - Head disc present. Head dorsum flat with gently concave frontal carinae. Frontal carinae strongly crenulate, expanded anteriorly, not covering the eyes, strongly converging posteriorly and connected by a short, straight carina on the vertex. Vertexal angles obtuse and with crenulate margin. Ocelli close to the posterior border of the head disc. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma. Anterior pronotal border straight. Scapular angles short but visible. Humeral angles with a triangular spine converging posteriorly and connected to the pronotal crest which is developed. Pronotal sides posterior to the angles straight. Promesonotal suture im-

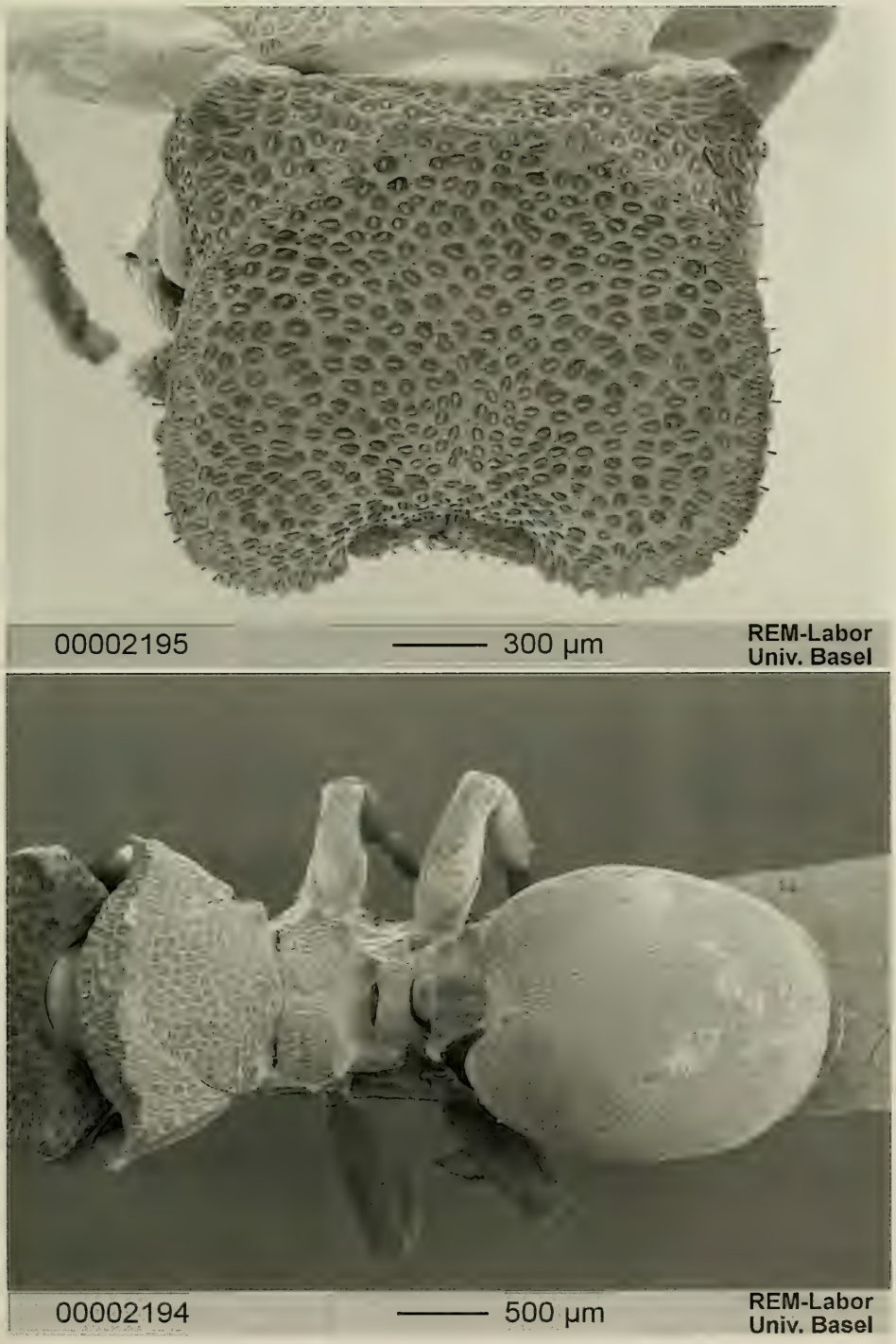


Fig. 248. *Cephalotes crenaticeps* (MAYR). Soldier from Venezuela (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 249. *Cephalotes crenaticeps* (MAYR). Gyne from Ar. Rancho Grande, Venezuela): head (top) and meso- and metasoma (bottom) in dorsal view.

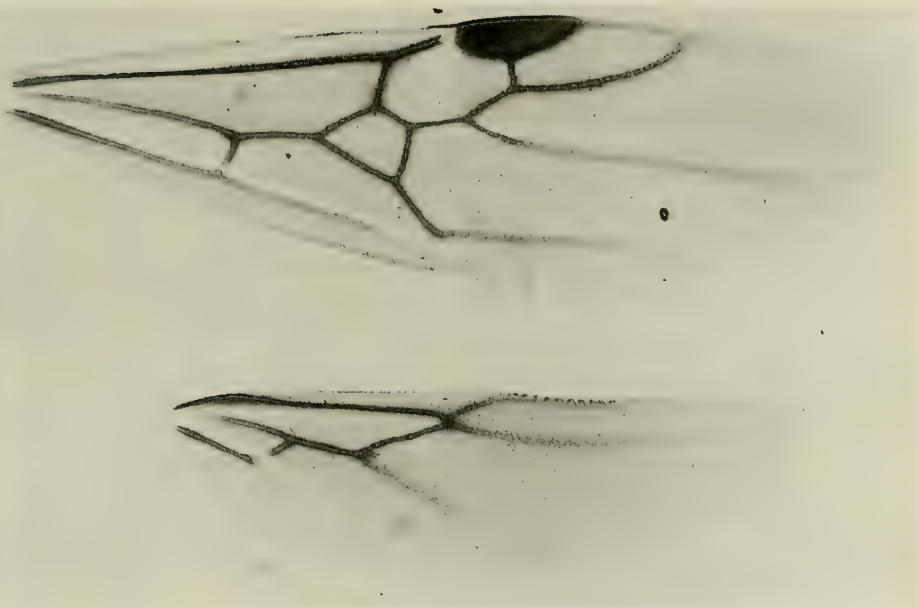


Fig. 250. *Cephalotes crenaticeps* (MAYR). Gyne from Venezuela (no further locality), fore and hind wings.

pressed. Lower mesopleurae with a denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face with two pairs of teeth, the first pair obtuse, the second pair thin, smaller than the first and curved forwards. Declivous face with the sides converging posteriorly.

Pedicel as in the soldier but with the spines less developed.

Legs and gaster as in the soldier, but the gaster longer.

Wings as in Fig. 250.

Sculpture. Head dorsum superficially reticulate and covered with round foveae, broader than their interspaces. Mesosoma reticulate and with oval foveae, denser and smaller on the scutellum and on the propodeum, sparser on the mesonotum. Ventral face of the head reticulate and with broad, dense, deep, oval foveae forming few, irregular rugosities. Declivous face of the propodeum reticulate only. Pleurae reticulate and with foveae, dense on the mesopleurae, sparser on the propleurae and rare on the metapleurae. Metapleurae with few, thin, longitudinal rugosities. Gaster reticulate and with minute, superficial foveae. Legs with the same sculpture as on the gaster but with the foveae deeper on the extensor face of the femora and tibiae. First gastral sternite shining in the middle.

Pilosity. As in the soldier but with the clubbed hairs sparse on the whole body.

Colour. As in the soldier.

Measurements (in mm) and indices: TL 8.04–8.32; HL 160–1.68; HW 1.64–1.72; EL 0.33–0.37; PW 1.60–1.70; PeW 0.58–0.64; PpW 0.75–0.80; HBaL 0.56–0.64; HBaW 0.15–0.17; CI 102.4–102.5; PI 97.6–105.0; PPeI 258.1–293.1; PPpI 210.5–224.0; HBaI 26.6–28.6.

Material examined. - **Venezuela**: no further locality, 14.VI.1949, ex. *Cattleya*, 7 workers, 3 soldiers, 2 gynes, J. ADAMS [USNM]; Ar. Rancho Grande, 27.VII.1967, 1 gyne, R. W. POOLE [MCZC]. Miranda: Altos de Pipe (IVIC), Los Teques, 03.III.1982, 1 worker, C. R. F. BRANDÃO & L. CAMPOS [MZSP].

Colombia: no further locality, 1 gyne (holotype) [NHMW].

D i s c u s s i o n . - KEMPF (1958 a) supposed *crenaticeps* (known only on the gyne at that time) to be similar to *coffeae*. A series of workers, soldiers (both previously undescribed) and gynes collected in Venezuela allows a better appreciation of the phylogenetic position of *crenaticeps*. There seem to be no close relationship between this species and *coffeae*.

The workers of *crenaticeps* differ from those of *ecuadorialis* (its sister species) by the yellow spot on the first gastral tergite not reaching the posterior border, by the narrower membranaceous expansions of the vertexal angles, by the frontal carinae weakly upturned over the eyes and by the absence of membranaceous expansions of the first gastral tergite. The gyne from Ar. Rancho Grande (MCZC) has the foveae on the head disc slightly smaller than those of the other gynes examined during the present study.

D i s t r i b u t i o n : Venezuela and Colombia.

Cephalotes ecuadorialis DE ANDRADE new species
Fig. 251

T y p e m a t e r i a l : Holotype worker from Ecuador, Endese Forest Reserve, Pichincha Prov., 25.1.1994, L. E. Tennant. Paratype worker, same data as the holotype, both, holotype and paratype in MCZC.

D e r i v a t i o n o m i n i s : *ecuadorialis* is a neologism indicating the provenance of the species from Ecuador.

D i a g n o s i s . - A member of the *crenaticeps* clade differing from its sister species, *crenaticeps*, by the presence of gastral membranaceous expansions.

W o r k e r (Fig. 251). - Head subquadrate. Frons convex. Frontal carinae crenulate, upturned above the eyes. Vertexal angles broad, truncate, bearing a membranaceous expansion with strongly crenulate margin. Vertexal margin concave. Vertex with a pair of minute denticles. Mandibles with lateral carina.

Mesosoma. Scapular angles free. Anterior pronotal border gently convex. Pronotal sides with a pair of triangular, semi-membranaceous teeth converging posteriorly in an obtuse, short tooth. Promesonotal and propodeal sutures impressed on the sides in dorsal view. Mesonotum with a minute pair of denticles. Propodeum with differentiate basal and declivous faces; sides of the basal face medially denticulate; declivous face anterolaterally marked by a pair of minute denticles, the rest converging posteriorly.

Petiole. Anterior face truncate, posterior face flat. Petiolar sides diverging up to their mid-length, where they bear a pair of small denticles strongly converging posteriorly. Postpetiole gently convex dorsally; postpetiolar spines directed slightly forwards at the base and curved backwards at the apex.

Gaster. Oval with a pair of anterolateral, narrow, membranaceous expansions not reaching the stigma posteriorly.

Hind femora without angle or denticles in the middle. Hind basitarsi long, flat and slightly broader at the base.

Sculpture. Head, mesosoma and pedicel reticulate and covered by foveae broader than their interspaces, slightly denser on the vertexal angles and mesosoma, smaller and superficial on the pedicel. Frontal carinae reticulate and rarely foveolate. Ventral face of the head reticulate, with faint, longitudinal rugulae and with superficial, oval foveae denser on the anterior half. Declivous face of the propodeum and propleurae longitudinally rugulose and with few, superficial foveae. Meso- and metapleurae reticulate and superficially foveolate. Gaster strongly reticulate and with superficial, minute foveae. Anterior third of the first gastral sternite and sides of the remaining two thirds covered with longitudinal, posteriorly concentric rugosities. Middle of the first gastral sternite superficially shining. Legs with the same sculpture as on the gaster but with the foveae more impressed on the extensor face of femora and tibiae. Internal face of the hind coxae with longitudinal, thin rugae.

Pilosity. Each fovea with an appressed hair. Sides of the frontal carinae and of the mesosoma, pedicel and first gastral tergite with clubbed hairs, rare on the mesosoma andpedicel. Similar hairs or slightly longer on the border of the remaining gastral segments and on the legs. First gastral sternite and border of the remaining sternites with rare, long, pointed hairs.

Colour. Dark brown, opaque, with lighter extensor face of the tibiae. Frontal carinae yellowish to light brown and semi-transparent. Membranaceous expansion of the vertexal border and of the gaster, apex of the pronotal teeth and of the postpetiolar spines light brown. First gastral tergite with a pair of oval, anterolateral, orange spots almost reaching the posterior border.

Measurements (in mm) and indices: TL 4.80–4.88; HL 1.16–1.18; HW 1.28–1.30; EL 0.31; PW 1.10; PeW 0.46; PpW 0.55–0.57; HBaL 0.55; HBaW 0.14; CI 110.2–110.3; PI 116.4–118.2; PPeI 239.1; PPpI 193.0–200.0; HBaI 25.4.

G y n e (tentative attribution). - Head slightly longer than broad. Disc present. Head dorsum convex posteriorly and slightly flat anteriorly. Frontal carinae strongly crenulate, expanded anteriorly, not covering the eyes, converging posteriorly and connected by a short, straight margination on the vertex. Vertexal angles obtuse and with crenulate margin. Ocelli distant from the posterior border of the disc. Mandibles laterally carinate.

Mesosoma. Anterior pronotal border convex. Humeral angles with a pair of pointed teeth. Pronotal sides straight. Pronotal carina impressed and interrupted only medially. Lower mesopleurae with a stout denticle. Mesonotum and scutellum flat. Propodeum with differentiate basal and declivous faces; sides of the basal face gently convex anteriorly, with a pair of teeth curved forwards. Declivous face with posteriorly converging sides.

Petiole with oblique anterior face and straight posteriorly; petiolar sides with a minute denticle medially. Postpetiole convex; postpetiolar sides with a pair of spines directed slightly forwards at the base and curved backwards at the apex.

Mid and hind femora not angulate. Mid and hind basitarsi flat and slightly broad at the base.

Gaster with a pair of anterolateral lobes.

Sculpture. Head dorsum superficially and minutely punctate and covered with small, superficial foveae, broader than their interspaces; frontal carinae superficially shining. Ventral part of the head minutely punctate and covered with foveae larger and less regular than those on the dorsum, denser on the sides. Pronotum, mesonotum, scutellum and upper mesopleurae strongly punctate and with variably clumped foveae. Basal face of the propodeum and pedicel strongly punctate and with dense, irregular foveae. Propleurae, lower mesopleurae and metapleurae strongly punctate and with rare, superficial foveae. Declivous face of the propodeum, legs and first tergite and sternite reticulate punctate. Anterior third of the first gastral tergite with longitudinal, irregular, thin rugosities. Remaining tergites, sternites and middle of the first gastral sternite superficially reticulate, punctate and shining.

Pilosity. Body with four type of hairs: (1) appressed, canaliculate, originating from the foveae; (2) thinner than those originating from the foveae and appressed, on the gaster and on the legs; (3) suberect, sparse and clubbed on the sides of the frontal carinae, on the vertexal angles, on the mesosoma, on the pedicel, on the gaster and on the legs; (4) long, truncate, subdecumbent on the posterior border of the tergites and of the sternites.

Colour. Dark brown with lighter legs. Frontal carinae dark ferruginous and barely semi-transparent. First gastral tergite with two pairs of yellow spots, the first pair on the anterior third and surpassing the stigma posteriorly and the second pair laterally, on the posterior third.

Measurements (in mm) and indices: TL 9.00; HL 164; HW 1.64; EL 0.36; PW 1.52; PeW 0.65; PpW 0.80; HBaL 0.71; HBaW 0.22; CI 100.0; PI 107.9; PPeI 233.8; PPpI 190.0; HBaI 31.0.

M a t e r i a l e x a m i n e d . - **Ecuador**: Paramba, NW of Ecuador, 3500', March 1897, 1 gyne, W. F. H. ROSENBERG S. [ZSMC]. P i c h i n c h a : Endese Forest Reserve, 25.1.1994, 2 workers (holotype and paratype) L. E. TENNANT [MCZC].

D i s c u s s i o n . - *C. ecuadorialis* is the sister species of *crenaticeps*. Both share the first gastral tergite with a pair of yellow-orange spots and the first gastral sternite

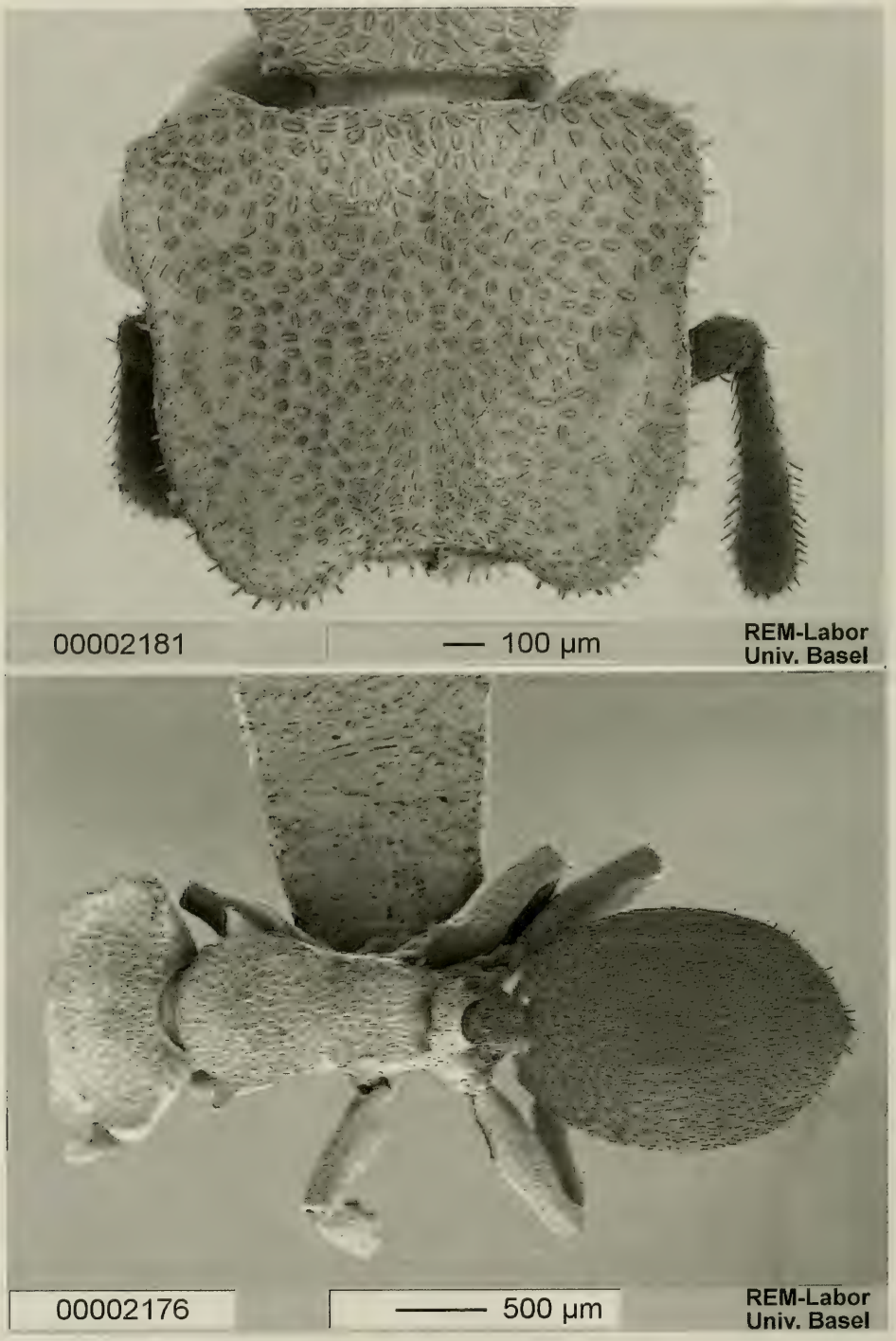


Fig. 251. *Cephalotes ecuadorialis* DE ANDRADE. Worker from Endese Forest Reserve (Pichincha), Ecuador: head (top) and meso- and metasoma (bottom) in dorsal view.

laterally with longitudinal rugosities, two characters unique to *ecuadorialis* and *crenaticeps* among closely related species, but appearing homoplastically in other clades as well. *C. ecuadorialis* differs from *crenaticeps* by the frontal carinae much more upturned over the eyes, by the broader vertexal angles, by the first gastral tergite with a narrow membranaceous expansion and with a pair of yellow-orange spots almost reaching the posterior border (shortly surpassing the stigma in *crenaticeps*). The attribution of the gyne from Paramba to this species is an easy conjecture which is not contrasted by morphological characters and is supported by the geographic proximity of the localities where workers and gyne have been collected. It needs, however, confirmation.

Distribution. - Ecuador.

5.6. 17. The *coffeae* clade

A relatively large clade containing 11 species, 7 of which are fossil. It is characterised by two synapomorphies, both secondarily lost in some specialised species: postpetiole with broad lateral expansions and first gastral sternite simply reticulate (the synapomorphic state is the secondary loss of striation). There is, however, another potential synapomorphy for these species not resulting from our list of characters and worth to be mentioned in this context: the presence of abundant standing hairs on the gaster well visible in the Recent *setulifer*, *peruviensis*, *trichophorus* and *coffeae* and in the fossils *alveolatus*, *sucinus* and *obscurus*. The general habitus of all these species, however, is very homogeneous and different from that of the other *Cephalotes* species. The species belonging to this clade are in part fossil, either Mexican or Dominican, or confined to Central and Northern South America. The workers of three fossil species (*dieteri*, *sucinus*, and *integerrimus*) share also a darker spot in the center of the first gastric tergite but this character is difficult to appreciate in the amber specimens even within different individuals of the same species.

Species included in the clade: *alveolatus*, *bloosi*, *coffeae*, *dieteri*, *integerrimus*, *obscurus*, *peruviensis*, *setulifer*, *sucinus*, *trichophorus*, *ventriosus*.

† *Cephalotes alveolatus* (VIERBERGEN & SCHEVEN) new combination
Figs. 7 A, B

Zacryptocerus alveolatus VIERBERGEN & SCHEVEN, 1995: 166, figs. 9 a-d. Worker. Dominican amber. Original description. Type material: holotype (unique) in the JSHC, examined.

Diagnosis. - A member of the *coffeae* clade characterised, in the worker, by the body with abundant, erect, clubbed hairs.

Worker. - Head subquadrate. Frontal carinae crenulate and not upturned above the eyes. Vertexal angles broad, truncate and with superficially crenulate margin. Vertexal margin concave. Vertex with a pair of denticles. Mandibles laterally angulate.

Mesosoma. Scapular angles absent or not visible in dorsal view. Anterior pronotal border straight, protruding anteriorly and passing into the sides with a long, weak concavity. Pronotal sides with a pair of broad, long, anteriorly truncate and posteriorly converging lamellae with semi-transparent border. Promesonotal suture weakly marked. Sides of the mesonotum armed with a pair of round or obtuse teeth. Propodeal suture impressed. Propodeum with differentiate basal and declivous faces; sides of the basal face delimited anteriorly and posteriorly by an angle or by small denticles; declivous face of the propodeum converging posteriorly.

Petiole. Anterior face truncate; posterior face convex. Petiolar sides, medially, with a pair of obtuse denticles. Postpetiole convex and with a laterally carinate median sulcus; anterior half of the postpetiolar sides with a pair of round teeth arising from the anterior border of the postpetiole and directed slightly forward.

Gaster suboval, with a pair of anterolateral, lamellae not surpassing the stigma posteriorly.

Fore coxae gently angulate. Mid and hind femora not angulate. Mid and hind basitarsi flat and broad at the base.

Sculpture. Head minutely punctate and densely covered with foveae on the posterior third; the foveae sparser, smaller and more superficial on the two anterior thirds. Ventral face of the head with the same type of sculpture as the anterior part of the head dorsum and superimposed by irregular, thin, longitudinal rugosities. Mesosoma and peduncular segments minutely reticulate-punctate and with dense foveae. Pleurae reticulate and with longitudinal, rugosities. First gastral tergite densely covered with broad reticulation-foveolation. Legs and first gastral sternite strongly reticulate; the same sculpture but less impressed on the remaining tergites and sternites.

Pilosity. Body with the following types of hairs: (1) appressed hairs originating from the foveae; similar hairs but not originating from foveae on the first gastral tergite and sternite; (2) short, clubbed hairs on the crenulation of the frontal carinae, on the border of the vertexal angles, on the sides of the mesosoma, and, denser, on the peduncular segments, on the gaster and on the legs; (3) hairs similar to type (2) but thinner and longer sparse on the gastral sternites; (4) rare, long, pointed hairs on the gastral sternites.

Colour. Based on the specimen DO–1980 (altered by burning in the holotype): frontal carinae, vertexal angles and border of the pronotal lamellae black; anterolateral lamellae of the gaster ferruginous and semi-transparent. The gastral lamellae appear slightly dark ferruginous in the holotype.

Measurements (in mm) and indices: TL 5.56–6.32; HL 1.32–1.46; HW 1.64–1.88; EL 0.34–0.36; PW 1.52–1.72; PeW 0.54–0.56; PpW 0.56–0.64; HBaL 0.56–0.60; HBaW 0.24; CI 124.2–128.8; PI 107.9–109.3; PPeI 281.5-307.1 PPpI 268.7–271.4; HBaI 40.0–42.8.

Material examined. - **Dominican amber**: 1 worker (holotype) in the JSHC; 1 worker in the SMNS (reference number: Do–1980).

Discussion. - *C. alveolatus* in our cladogram results as the outgroup of all the remaining species of the *coffeae* clade. *Alveolatus* shares with *ventriosus*, *sucinus* and *obscurus* the vertex with a pair of denticles and differs from these three species for having the hind femora not angulate. *C. alveolatus* is the sole species of the clade with abundant clavate hairs. Though we have no doubts on the cospecificity of the two specimens we attribute to this species, the SMNS specimen differs from the holotype in some microsculptural details the most visible of which are longitudinal rugosities on the basal face of the propodeum and the strong reticulation-punctuation on the first gastral tergite.

Distribution: Dominican amber.

† *Cephalotes ventriosus* DE ANDRADE new species
Figs. 14 B, 252

Type material: Holotype worker (unique) in the Mexican amber sample Mx-391 in the SMNS.

Derivatio nominis: from the Latin *ventriosus* (= big-bellied) referred to the large size of the gaster.

Diagnosis. - A member of the *coffeae* clade differing from *alveolatus* by having only a few clavate hairs, and from *sucinus* and *obscurus* by the pronotal lamellae incised (instead of continuous).

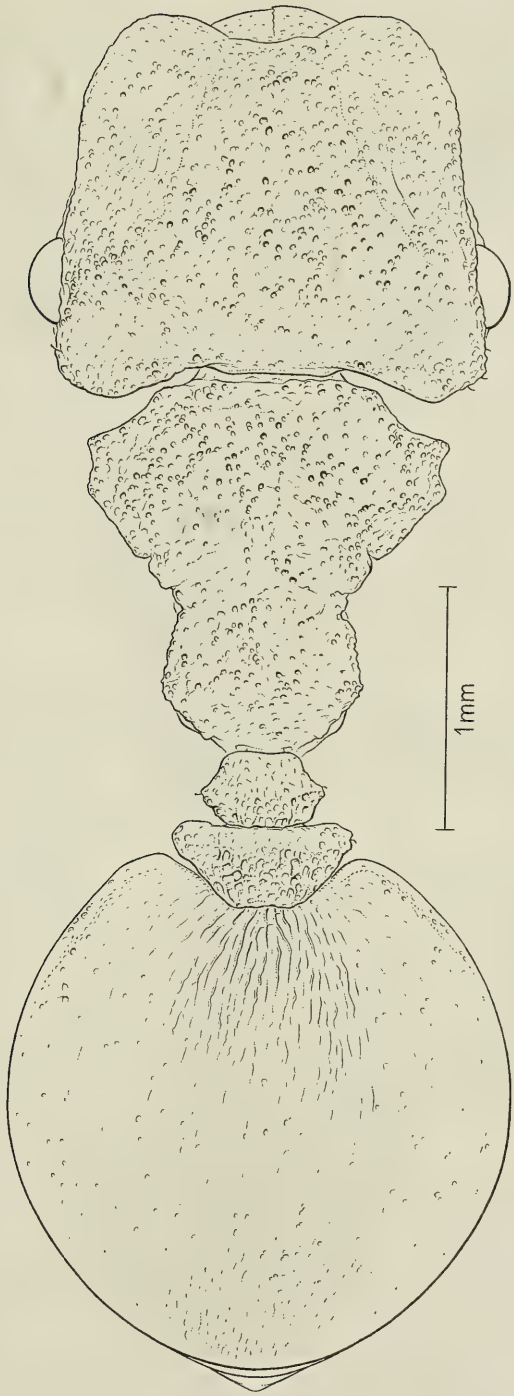


Fig. 252. *Cephalotes ventriosus* DE ANDRADE from Mexican amber. Worker in dorsal view. Appendages omitted.

W o r k e r (Fig. 252). - Head broader than long. Frontal carinae superficially crenulate and upturned above the eyes. Vertexal angles broad, truncate to round and with superficially crenulate margin. Vertexal margin concave. Vertex with a pair of denticles. Mandibles laterally angulate.

Mesosoma. Scapular angles visible. Pronotum with a pair of lamellae with semi-transparent border broad, long, anteriorly incised and converging posteriorly. Promesonotal suture weakly impressed. Mesonotum with a pair of broad, truncate teeth. Propodeal suture impressed. Propodeum with differentiate basal and declivous faces; sides of the basal face delimited anteriorly and posteriorly by an angle.

Anterior face of the petiole truncate; its sides with a pair of small denticles. Postpetiole convex, subtrapezoidal in dorsal view and with a pair of round, solid expansions directed laterally.

Gaster globose, with a pair of anterolateral, lamellae reaching the stigma posteriorly.

Fore coxae angulate. Hind femora angulate. Mid and hind basitarsi flat and broad at the base.

Sculpture. Head and mesosoma minutely punctate and with variably clumped, small foveae more superficial on the frontal carinae. Pleurae reticulate and with few, longitudinal rugosities. Pedicel punctate and foveolate, the foveae larger on the postpetiole. Gaster punctate and covered by broad, thin reticulation; this structure less impressed on the center of the first gastral sternite. Anterior half of the first gastral tergite with additional, longitudinal rugosities.

Pilosity. Body with the following types of hairs: (1) short, rare, clubbed hairs on the frontal carinae, on the border of the vertexal angles, on the sides of the petiole and postpetiole, on the posterior border of the terminal tergites and on the legs; (2) rare, long, pointed hairs on the gastral sternites.

Colour. Black. Frontal carinae, expansions of the vertexal angles, and pronotal lamellae brown.

Measurements (in mm) and indices: TL 6.10; HL 1.38; HW 1.80; EL 0.36; PW 1.50; PeW 0.52; PpW 0.75; HBaL 0.50; HBaW 0.16; CI 130.4; PI 120.0; PPeI 288.5; PPpI 200.0; HBaI 32.0.

M a t e r i a l e x a m i n e d . - **Mexican amber**: 1 worker (holotype) [Mx-391, SMNS].

D i s c u s s i o n . - *C. ventriosus* is remarkable for the globose gaster. There seems to be no Recent species closely related to it since *ventriosus* appears basally in a clade containing mostly fossil species. For the general habitus the Recent species recalling at most *ventriosus* is *patei*. The two, however, cannot be closely related since each of them lacks the synapomorphies already listed under the respective clades. It is not impossible, nonetheless, that the discovery of the soldier of *ventriosus* could modify our current reconstruction of its phylogenetic position.

D i s t r i b u t i o n : Mexican amber.

† *Cephalotes sucinus* DE ANDRADE new species

Figs. 13 A-C, 253

T y p e m a t e r i a l : Holotype worker (unique) in the Dominican amber sample H 10–118 in the GOPC.

D e r i v a t i o n o m i n i s : *Sucinus* in Latin means made of amber.

D i a g n o s i s . - A member of the *coffeae* clade differing from its sister species, *obscurus*, by the sparser body foveae.

W o r k e r (Fig. 253). - Head slightly broader than long. Vertexal angles round. Vertex with denticles. Vertexal margin gently concave. Mandibles laterally angulate.

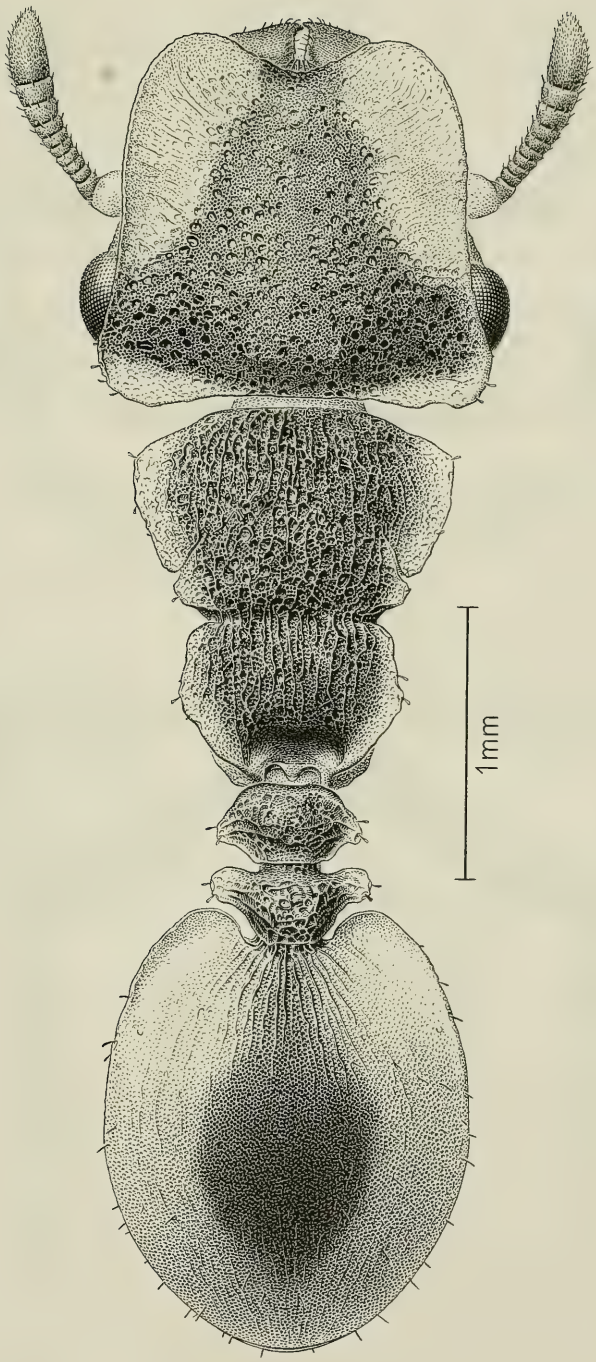


Fig. 253. *Cephalotes sucinus* DE ANDRADE from Dominican amber. Worker in dorsal view. Appendages omitted.

Mesosoma. Scapular angles absent or not visible in dorsal view. Anterior pronotal border gently convex. Pronotal sides with a broad, long, continuous lamella. Promesonotal suture weakly marked. Sides of the mesonotum armed with a pair of truncate teeth. Propodeal suture impressed. Propodeum flat dorsally, bearing a lamellaceous expansion narrower than the pronotum and medially angulate. Basal and declivous faces differentiate.

Petiole. Anterior face truncate. Petiolar dorsum gently convex; petiolar sides with a small, stout tooth curved backwards. Postpetiole convex; postpetiolar sides anteriorly with a broad, round expansion.

Gaster suboval and with a pair of anterolateral lamellae not surpassing the stigma posteriorly.

Fore coxae angulate. Mid and hind femora angulate. Mid and hind basitarsi flat and with broad base.

Sculpture. Head minutely reticulate and with variably clumped foveae, smaller and shallower on the anterior half. Mesonotum reticulate and with foveae superimposed to irregular, thin, slightly longitudinal rugosities. Peduncular segments reticulate and with small foveae superimposed to irregular rugosities. Pleurae, gastral tergites and legs strongly reticulate and with short, longitudinal rugosities; the reticulation more superficial on the sternites.

Pilosity. Each fovea with a thin, appressed hair. Border of the vertexal angles, of the mesosoma, of the peduncular segments, gaster and legs with sparse, short, clubbed hairs. First gas-tral sternite with additional rare, suberect, pointed, long hairs.

Colour. Frontal carinae, vertexal angles, border of the mesonotal lamellae and gastral lamellae orange to ferruginous. Head, mesosoma and peduncular segments brown. Gaster and legs ferruginous. First gastral tergite anterolaterally with a pair of light yellow spots. First gastral tergite and sternite medially with a large brown spot.

Measurements (in mm) and indices: TL 4.96; HL 1.16; HW 1.40; EL 0.32; PW 1.18; PeW 0.52; PpW 0.60; HBaL 0.38; HBaW 0.15; CI 120.7; PI 118.6; PPeI 215.4; PPpI 186.7; HBaI 39.5.

Material examined. - **Dominican amber**: 1 worker (holotype) [H 10–118, GOPC].

Discussion. - *C. sucinus* shares with its sister species *obscurus* the scapular angles not visible in dorsal view. These two species are very similar in general habitus but they are very different in sculpture.

Distribution: Dominican amber.

† *Cephalotes obscurus* (Vierbergen & Scheven) new combination
Figs. 16 C, D, 254, 255

Zacryptocerus obscurus Vierbergen & Scheven, 1995: 164, fig. 8. Worker. Dominican amber. Original description. Type material: holotype (unique) in the MCZC, examined.

Diagnosis. - A member of the *coffeae* clade differing from its sister species, *sucinus*, by the denser body foveae.

Worker (Figs. 254, 255). - Head subquadrate. Frontal carinae superficially crenulate and not upturned above the eyes. Vertexal angles broad, round to slightly truncate and with weakly crenulate margin. Vertexal margin gently concave medially. Vertex with a pair of denticles. Mandibles laterally angulate.

Mesosoma. Scapular angles absent or not visible in dorsal view. Anterior pronotal border straight, protruding anteriorly and passing into the sides with a long, weak concavity. Pronotal sides with a broad, long, continuous lamella with semitransparent border. Promesonotal suture superficially marked in the holotype only. Sides of the mesonotum armed with a pair of truncate or slightly round teeth. Propodeum with differentiate basal and declivous faces; sides of the basal face delimited anteriorly and posteriorly by an angle or by

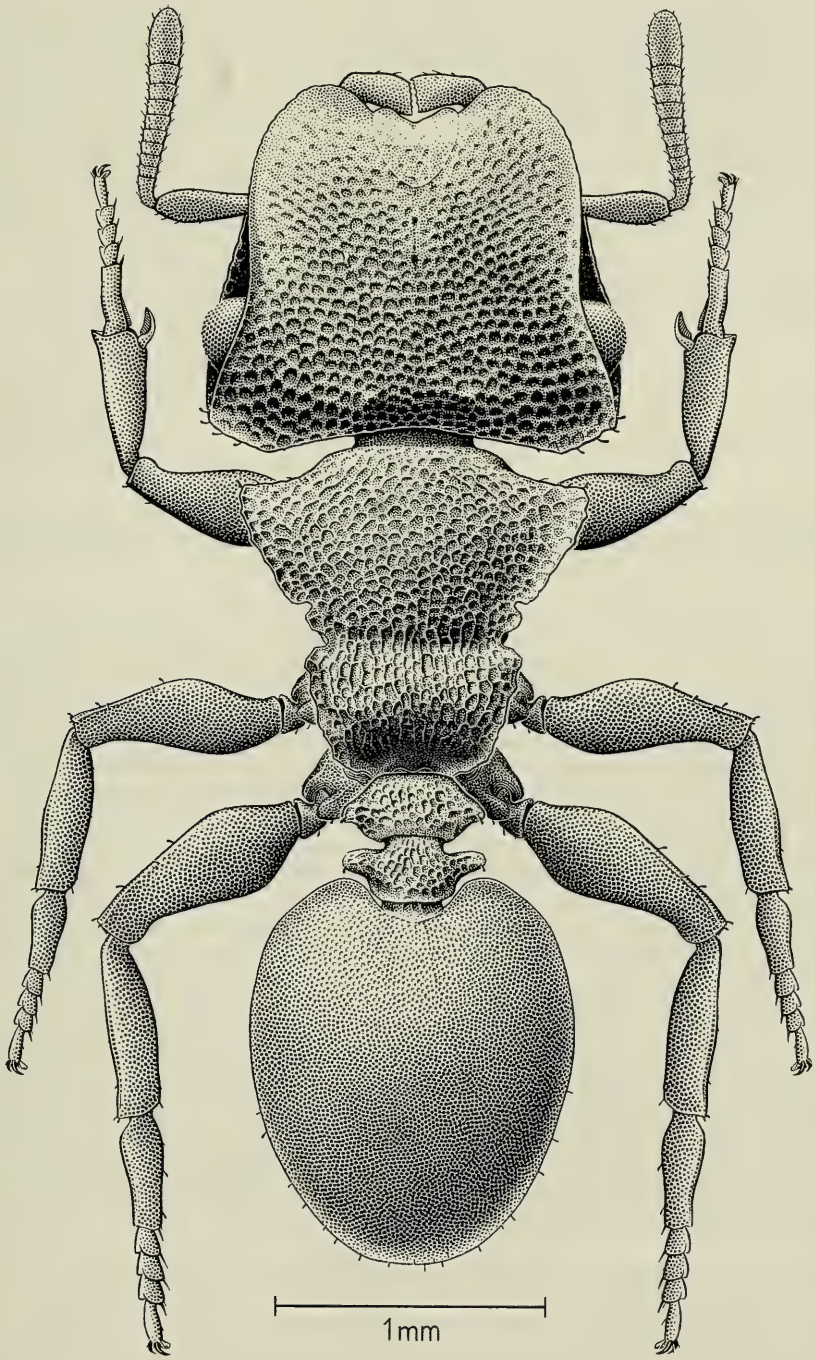


Fig. 254. *Cephalotes obscurus* (VIERBERGEN & SCHEVEN) from Dominican amber. Worker in dorsal view.

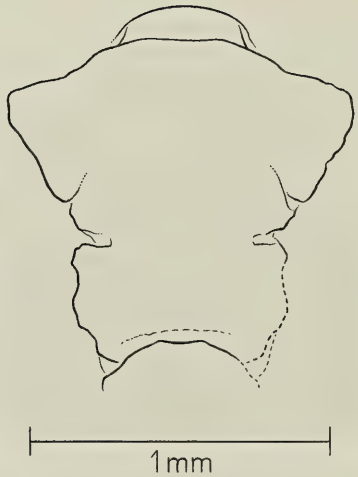


Fig. 255. *Cephalotes obscurus* (VIERBERGEN & SCHEVEN) from Dominican amber. Worker mesosoma exemplifying another possible morphology. Transitional forms between the morphology illustrated here and that of Fig. 254 are frequent.

small, irregular denticles; declivous face of the propodeum converging posteriorly; an additional pair of small, irregular denticles on the middle of the declivous face of the propodeum visible in the holotype only.

Petiole. Anterior face truncate, posterior face superficially convex. Petiolar sides, medially, with a pair of small, obtuse or round teeth. Postpetiole convex in the middle; anterior half of the postpetiolar sides with a pair of broad, round teeth arising from the anterior border of the postpetiole and directed slightly forwards.

Gaster suboval, with a pair of anterolateral lamellae not surpassing the stigma posteriorly.

Fore coxae angulate. Mid and hind femora angulate. Mid and hind basitarsi flattened and broader at the base.

Sculpture. Head minutely reticulate-punctate and with dense foveae shallower, sparser and diminishing in size anteriorly. Ventral face of the head with the same type of sculpture as on the anterior part of the dorsum. Pronotum and mesonotum minutely reticulate-punctate and with foveae as on the posterior part of the head dorsum but with narrower interspaces. The reticulation becomes strongly longitudinally oriented on the propodeum. Pedicel with the same type of sculpture as the pronotum but with smaller foveae. Gastral tergites, sides of the first gastral sternite, remaining sternites and legs strongly reticulate. Center of the first gastral sternite shining.

Pilosity. Each fovea with an appressed, minutely clavate hair; similar hairs on the gastral tergites and on the legs Border of the vertexal angles, of the pronotum, of the peduncular projections, legs and border of the gastral tergites and sternites with similar but suberect, clubbed hairs. Border of the first and second gastral sternites with rare, thin, erect, pointed hairs.

Colour. Frontal carinae, vertexal angles, pronotal lamellae and gastral lamellae ferruginous and semitransparent.

Measurements (in mm) and indices: TL 4.02–4.88; HL 0.98–1.16; HW 1.28–1.44; EL 0.27–0.30; PW 1.14–1.36; PeW 0.50–0.52; PpW 0.51–0.56; HBaL 0.38–0.42; HBaW 0.14; CI 124.1–130.6; PI 105.9–112.3; PPeI 228.0–261.5; PPpI 223.5–242.8; HBaI 33.3–36.8.

Material examined. - **Dominican Amber**: 1 worker (holotype) [our reference number MCZC–9, MCZC]; 1 worker [Do–5487, SMNS]; 1 worker [PE 111, NHMB].

D i s c u s s i o n . - *C. obscurus* shares with some of its most closely related species, like *dieteri*, *integerrimus* and *bloosi* the propodeum unarmed (the specimens Do–5487 and PE 111) or with three small lateral denticles (the holotype) and the pronotal lamellae long and continuous. It can be distinguished from the other three fossil species by the presence of a pair of denticles on the vertex. The original description by VIERBERGEN & SCHEVEN (1995) mentions the absence of vertexal denticles. We observed such denticles reduced in size but present in all the specimens examined, including the holotype.

† *Cephalotes integerrimus* (VIERBERGEN & SCHEVEN) new combination
Figs. 12 A, C, D, 18 A, B, 256

- WAGENSBERG, 1995: n. n. fig. Worker.
- ANONYMOUS, 1995: n. n. fig. Worker.

Zacryptocerus integerrimus VIERBERGEN & SCHEVEN, 1995: 162, figs. 5 a-d. Worker. Dominican amber. Original description. Type material: holotype in the JSHC, examined.
- WAGENSBERG & SERRANO, 1997: n.n. fig. Worker.

D i a g n o s i s . - A member of the *coffeae* clade differing from its sister species, *dieteri*, by the sparser foveolation of the integument and by the CI $\geq$ 120.0 instead of < 114.

W o r k e r (Fig. 256). - Head slightly broader than long, with subparallel sides. Frontal carinae superficially crenulate, not upturned above the eyes. Vertexal angles round or slightly truncate. Vertexal margin concave. Mandibles laterally angulate.

Mesosoma. Scapular angles visible in dorsal view. Anterior pronotal border gently convex. Pronotal sides with a broad, long, continuous lamella. Promesonotal suture superficially marked in some specimens only. Sides of the mesonotum with a pair of round teeth. Propodeum with differentiate basal and declivous faces; sides of the basal face angulate anteriorly and pos-teriorly; declivous face of the propodeum converging posteriorly, sometimes a minute denticle in the middle of the sides of the declivous face.

Petiole. Anterior face truncate, posterior face flat. Petiolar sides with a pair of obtuse or pointed teeth medially. Postpetiolar node weakly concave in the middle; anterior half of the postpetiolar sides with a pair of obtuse to pointed teeth arising from the anterior border of the postpetiole and with the base slightly directed forwards.

Gaster sub-oval, with a pair of anterolateral, semitransparent lamellae reaching the stigma posteriorly.

Fore coxae angulate. Mid and hind femora angulate. Mid and hind basitarsi flat and with broad base.

Sculpture. Head minutely reticulate-punctate and with small foveae variably clumped. Ventral face of the head with the same type of sculpture as the dorsum but the reticulation less deep and slightly shining. Mesonotum reticulate-punctate and with foveae larger than those of the head and variably clumped. Declivous face of the propodeum and pleurae reticulate. Pedicel reticulate-punctate and with dense, superficial foveae of variable size. Some specimens with the foveae broader than their interspaces. Gastral tergites, sides of the first gastral sternite, remaining sternites and legs strongly reticulate. Center of the first gastral sternite shining.

Pilosity. Each fovea with a thin, appressed hair; similar hairs but thinner on the first gastral tergite and sternite and on the legs. Anterior border of the frontal carinae with rare pointed hairs. Border of the vertexal angles with short truncate hairs. Posterior sides of the first gastral tergite, posterior border of the remaining tergites and sternites with rare clubbed hairs of different length. Border of the gastral sternites, additionally, with rare, thin, erect, pointed hairs.

Colour. Frontal carinae, vertexal angles and gastral lamellae ferrugineous to brown and semitransparent. The transparency, of course, can not be observed in the specimens covered by a gaseous layer. At least in one specimen (MCZC–24) a darker spot in the middle of the first gastral tergite is well visible.

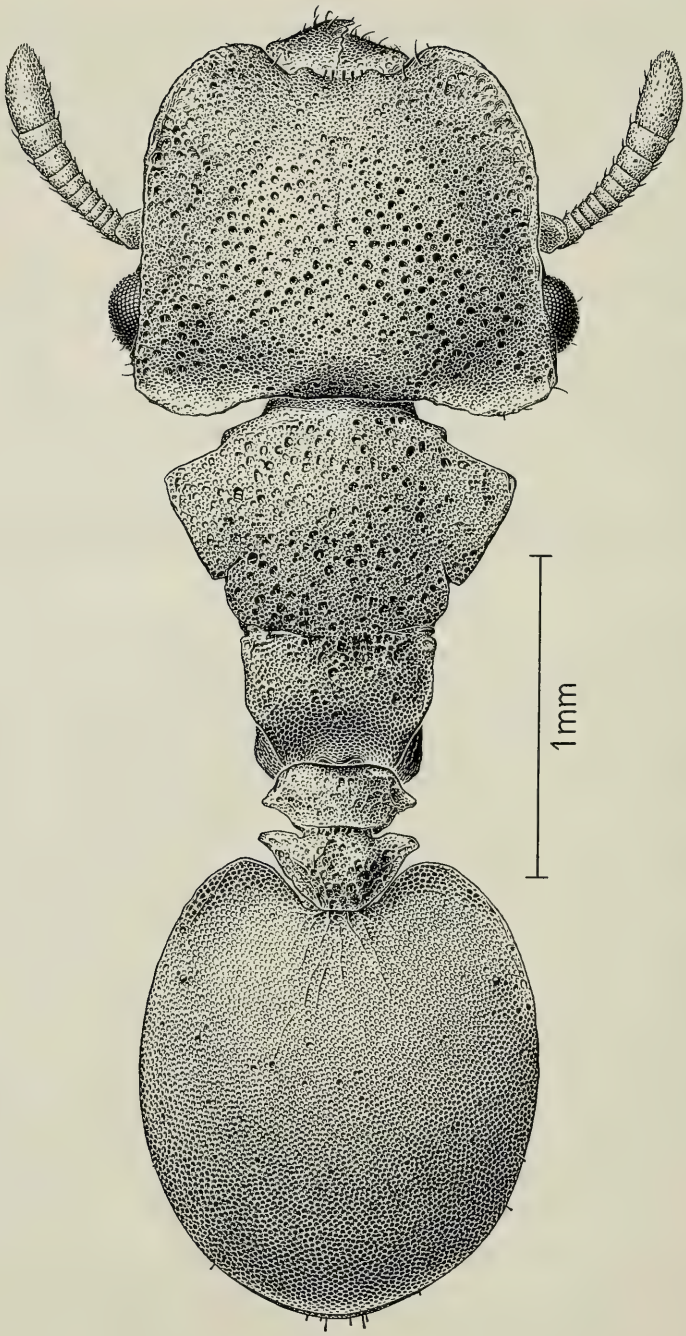


Fig. 256. *Cephalotes integerrimus* (VIERBERGEN & SCHEVEN) from Dominican amber. Worker in dorsal view. Appendages omitted.

Measurements (in mm) and indices: TL 3.78–4.06; HL 0.92–1.04; HW 1.12–1.32; EL 0.26–0.28; PW 0.92–1.06; PeW 0.40–0.50; PpW 0.46–0.52; HBaL 0.32–0.33; HBaW 0.13–0.14 CI 120.0–139.1; PI 112.0–134.8; PPeI 209.1–250.0; PPpI 200.0–225.5; HBaI 39.4–42.4.

Material examined. - **Dominican amber**: 1 worker (holotype) [JSHC]; 4 workers [Do-3326, Do-3792, Do–4479, Do–4711, SMNS]; 1 worker [our reference number MCZC–10, MCZC–15 from the mine El Valle, MCZC–17, MCZC–24, MCZC]; 1 worker (0025, MCCB).

Discussion. - *C. integerrimus* is the sister species of *dieteri*. Both species, together with their close relative, the Recent *trichophorus*, are among the smallest of the genus, with a size range paralleled only by the distantly related Recent *minutus* and *maculatus*.

The amber from El Valle where one of these specimens has been collected should be 20-30 Ma old (POINAR, 1992).

Distribution. - Dominican amber.

† *Cephalotes dieteri* BARONI URBANI new species
Figs. 16 A, B, 257

Type material: Holotype and paratype workers in the Dominican amber sample Do–618 and Do–4162, both in the SMNS.

Derivatio nominis: This species is named after Dr. Dieter Schlee who built up the Stuttgart amber collection which represents the most important source of fossil material for this study.

Diagnosis. - A member of the *coffeae* clade differing from its sister species, *integerrimus*, by the denser foveae and by the CI < 114.0.

Worker (Fig. 257). - Head slightly broader than long. Frontal carinae with superficially crenulate margin. Vertexal angles truncate and with crenulate border. Vertex without denticles. Vertexal margin concave. Mandibles laterally angulate.

Mesonotum. Scapular angles visible in dorsal view. Pronotum with a narrow, long, continuous lamella. Promesonotal suture superficially impressed. Mesonotum unarmed. Propodeal suture impressed. Propodeum with differentiate basal and declivous faces; propodeal sides unarmed.

Petiole slightly narrower than the postpetiole. Anterior face of the petiole truncate; petiolar dorsum almost flat; petiolar sides with a small, pointed tooth. Postpetiole gently concave medially; postpetiolar sides anteriorly with a triangular tooth.

Gaster suboval and with a pair of anterolateral lamellae

Fore coxae angulate. Hind femora angulate. Mid and hind basitarsi flat and with slightly broad base.

Sculpture. Head minutely reticulate and with dense foveae, shallower on the anterior half. Ventral face of the head with sculpture similar to the one of the dorsum but with rarer and shallower foveae. Mesonotum reticulate and with larger and denser foveae than those on the head dorsum; the foveae smaller, shallower and rarer on the declivous face of the propodeum. Pleurae simply reticulate. Pedicel sculptured as the declivous face of the propodeum. Gaster and legs strongly reticulate.

Pilosity. Each fovea with an appressed canaliculate hair; similar hairs but not originating from foveae and thinner on the gaster and on the legs. Posterior borders of the distal gastral segments with rare clubbed hairs. Second gastral tergite with a pair of long, thin, pointed hairs.

Colour. Frontal carinae, vertexal angles, border of the pronotal lamellae and gastral lamellae lighter.

Measurements (in mm) and indices: TL 3.22-3.48; HL 0.80-0.88; HW 0.91-1.00; EL 0.23; PW 0.72-0.86; PeW 0.33-0.37; PpW 0.35-0.41; HBaL 0.29-0.30; HBaW 0.10-0.11; CI 113.6-113.7; PI 116.3-126.4; PPeI 218.2-232.4; PPpI 205.7-209.7; HBaI 34.5-36.7.

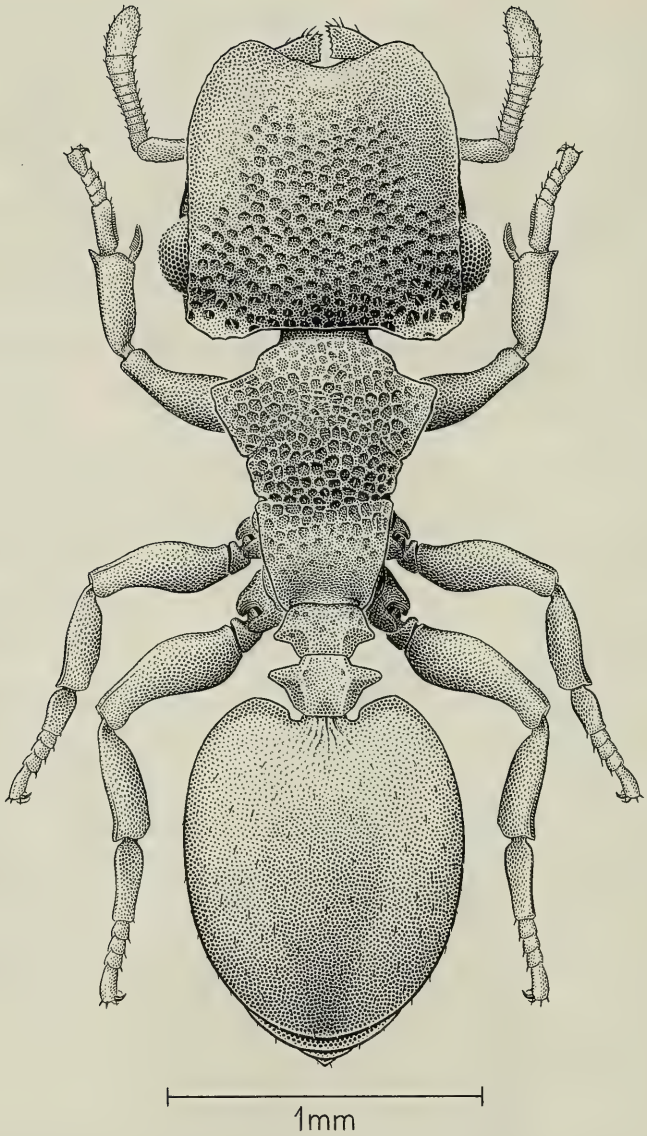


Fig. 257. *Cephalotes dieteri* BARONI URBANI from Dominican amber. Worker in dorsal view.

Material examined. - **Dominican amber**: 2 workers (holotype and paratype) [Do–618 and Do–4162, SMNS].

Discussion. - The closest Recent relative of *C. dieteri* and of its sister species *integerrimus*, is *trichophorus*. This similarity is stronger between *dieteri* and *trichophorus* which share also a very similar integumental sculpturation. The holotype and paratype specimens are very similar to each other.

Distribution: Dominican amber.

† *Cephalotes bloosi* Baroni Urbani & de Andrade new species

Figs. 14 C, 258

Type material: Holotype worker (unique) in Dominican amber sample H 10–119 in the GOPC.

Derivatio nominis: This species is named after Dr. Gert Bloos, the Editor of this and of most of our papers on amber ants for the numerous, necessary corrections he made on our manuscripts and for the self-control with which he called our attention on our faults.

Diagnosis. - A member of the *coffeae* clade characterised, in the worker, by the vertex without denticles, by the pronotum with a broad, continuous lamella and by the propodeum with three small, lateral denticles.

Worker (Fig. 258). - Head slightly broader than long. Frontal carinae with superficially crenulate border. Vertexal angles round and with crenulate border. Vertex without denticles. Vertexal margin concave. Mandibles laterally angulate.

Mesosoma flat in profile. Scapular angles visible in dorsal view. Pronotal sides with a broad, long, continuous lamella. Promesonotal suture absent Sides of the mesonotum armed with a pair of truncate teeth. Propodeal suture impressed. Propodeum with differentiate basal and declivous faces; propodeal sides with three small denticles.

Petiole slightly narrower than the postpetiole. Anterior face of the petiole truncate; petiolar dorsum almost flat; petiolar sides with a small weakly pointed tooth. Postpetiole gently convex, slightly concave medially; postpetiolar sides anteriorly with a broad, round tooth.

Gaster suboval and with a pair of narrow, anterolateral lamellae

Fore coxae angulate. Mid and hind femora angulate. Mid and hind basitarsi flat and with slightly broad base.

Sculpture. Head minutely reticulate and with superficial foveae variably clumped, small on the anterior and posterior fourths of the head and on the propodeum. Ventral face of the head superficially reticulate and with dense foveae on the anterior half. Peduncular segments reticulate and with dense foveae of variable size. Pleurae, first gastral tergite, sides of the first gastral sternite and legs strongly reticulate; middle of the first gastral sternite, remaining tergites and sternites superficially reticulate and shining. First gastral tergite with additional, minute, superficial foveae.

Pilosity. Each fovea with a thin, appressed hair; similar hairs not originating from foveae on the first gastral sternite. Border of the frontal carinae, of the vertexal angles, of the propodeum, of the peduncular segments, first gastral tergite and sternite, posterior border of the remaining tergites and sternites and legs with rare clubbed hairs slightly longer on the gaster. First gastral sternite with additional rare, suberect, pointed, long hairs.

Colour. Frontal carinae, vertexal angles, border of the pronotal lamellae and gastral lamellae brown.

Measurements (in mm) and indices: TL 4.54; HL 1.04; HW 1.27; EL 0.28; PW 1.04; PeW 0.50; PpW 0.52; HBaL 0.40; HBaW 0.12; CI 122.1; PI 122.1; PPeI 208.0; PPpI 200.0; HBaI 30.0.

Material examined. - **Dominican amber**: 1 worker (holotype) in the GOPC (reference number: H 10–119).

Discussion. - *C. bloosi* resembles, in pronotal morphology, two other Dominican fossils appearing in outgroup position in our cladogram: *dieteri* and *integerrimus*. On the other hand, by the presence of propodeal denticles and by the shape of the pedicel, *bloosi* is more similar to the four Recent Central American species appearing as its ingroups. This species represents, in a sense, a kind of morphological link between the Dominican amber and the Recent Neotropical faunas.

Although *bloosi* results as the fossil species closest to the Recent ones in this clade, it differs from all Recent species by a number of details and by the lack of two synapomorphies equally absent among all the other fossils: the denticulate (instead of continuous as in all fossils) pronotal lamella and the crenulate (not entire as in all

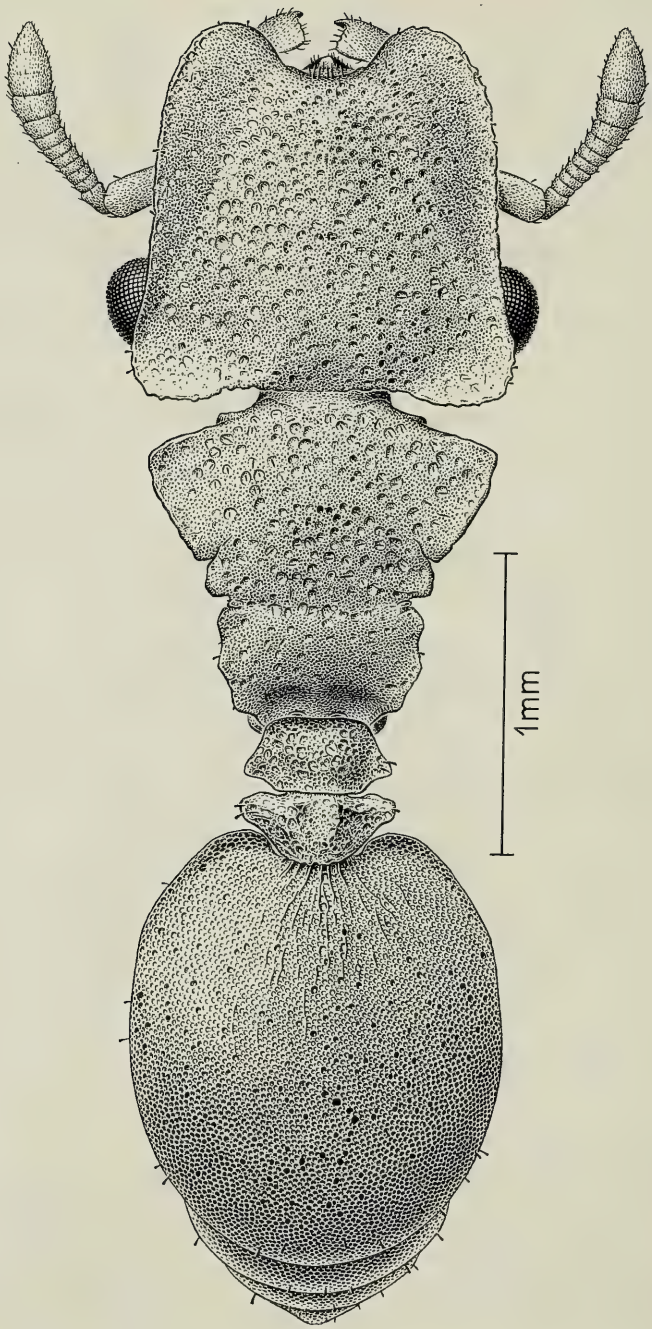


Fig. 258. *Cephalotes bloosi* BARONI URBANI & DE ANDRADE from Dominican amber. Worker in dorsal view. Appendages omitted.

fossils) postpetiolar expansions. The 7 fossil species of this clade, hence, appear morphologically more homogeneous by sharing a number of plesiomorphic traits.

Distribution: Dominican amber.

Cephalotes setulifer (EMERY) new combination
Figs. 259, 260, 384 D

Cryptocerus setulifer EMERY, 1894 a: 211, pl. 4, figs. 34-37. Worker, gyne. Original description. Type locality: Jiménez (Costa Rica). Type material: 2 syntype workers and 1 syntype gyne in the MCSN, labelled: "Jiménez, C. Rica", examined.

Cryptocerus setulifer orbis FOREL, 1906: 231. Worker and soldier. Original description. Type locality: El Hiquito near San Mateo (Costa Rica). Type material: 1 syntype worker and 1 syntype soldier in the MHNG, examined. Synonymy by KEMPF (1958 a: 146).

Cryptocerus setulifer EMERY, WHEELER, 1942: 211, pl. 53. Soldier, male.

Paracryptocerus setulifer (EMERY), KEMPF, 1958 a: 146, figs. 3, 4. Worker, soldier, gyne. First combination in *Paracryptocerus*.

Zacryptocerus setulifer, WHEELER & HÖLLDOBLER, 1984: 339, figs. 10–11. Soldier. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *coffeae* clade differing from *bloosi* by a number of traits already listed in the discussion of *bloosi*, and from *peruviensis* by the postpetiolar dorsum with two pairs of standing hairs (instead of one) and by the frontal carinae straight above the eyes; the soldier and gyne differ from all the other species of the clade by having the disc covering the mandibles.

Worker (Fig. 259) (description of KEMPF, 1958 a). - "Total length 3.4–4.4 mm; maximum length of head 1.00–1.18 mm; maximum length of thorax 1.03–1.25 mm. Black; the following testaceous: frontal carinae, tip of last funicular segment, tip of femora, extensor face of tibiae; ferruginous or reddish brown: apex of mandibles, edge of frontal carinae, tip of scape, funicular segment I, tarsites II - V, posterior border of gastral tergites; an oval pale testaceous or whitish spot on each of the anterior corners of the first gastral tergite.

Head opaque, subquadrate, its maximum length subequal to, or often slightly exceeding the interocular width. Supramandibular excision narrow. Clypeal sutures vestigial or absent. Anterior half of the usually noticeable crenulate frontal carinae obliquely converging cephalad, the lateral borders of head subparallel, rather straight, not excised in front, nor upturned above, eyes. Occipital lobes obliquely truncate. Occipital border gently emarginate. Dorsal face of head gently convex, finely but sharply punctate, more coarsely reticulate-rugose, the rugosities feeble discad, shallowly foveolate. Lower face of head finely reticulate-punctate, with sparse somewhat irregular longitudinal rugosities.

Thorax opaque, its anterior border gently arched. Scapular angle free, not incorporated in the lateral pronotal crest, lying somewhat below the anteriormost tooth of the pronotal crest, but perfectly visible when insect is viewed from the front. Lateral pronotal crest bidentate anteriorly, the first tooth more conspicuous, the second sometimes only vestigial, followed by an usually straight, seldom denticulate, crest, forming posteriorly an obtuse angle, before joining the mesonotum. Promesonotal suture vestigial or obsolete. Lateral lobe of mesonotum angulate or rounded, little projecting, usually not acutely dentate. Mesoepinotal suture impressed. Lateral border of epinotum tridentate, counting the feeble, subdentiform anterior corner and the usually minute, often only vestigial denticle at the junction of the declivous face. The second tooth most prominent. Entire thorax finely punctate, the dorsum also reticulate-rugose and foveolate. Sides of thorax with a few more or less horizontal rugosities on the laterotergite of pronotum and the bottom half of the pleura. Fore coxae not striate. Hind femora fusiform.

Peduncular segments opaque, finely punctate, densely but shallowly foveolate on dorsum. Petiole with a somewhat oblique, slightly shinier, anterior face, and a tooth on each side, facing obliquely caudad. Postpetiole flat on dorsum. Its lateral appendages more prominent, with rather strongly recurved tips (assuming the shape of an eagle's beak!).

Gaster opaque, oval. First gastral tergite finely and sharply punctured, its anterolateral lobes prominent and rounded, its lateral border marginate on the anterior half. First sternite reticulate-punctate, shinier, especially discad.

Standing hair long and flexuous on gastral sternites; shorter and straight posterolaterally and along the borders of the first gastral tergite; still shorter, and somewhat thickened on tip of thoracic and peduncular teeth, on the border of epinotum, sporadically, rare, not regularly dispersed, on the rest of the thoracic dorsum, sparse and oblique on legs; very short clavate at tip, along the crenulate border of frontal carinae and the lateral border of head, back to the occipital lobe. Scalelike, appressed, silvery or whitish, canaliculate, somewhat elongate hair very prominent in foveolae of dorsum of head, cheeks, dorsum of thorax, bottom half of pleura, dorsum of peduncle, extensor face of femora and tibiae; thinner, simple but still very conspicuous and relatively crowded on first gastral tergite."

Measurements (in mm) and indices: TL 3.64–4.60; HL 0.94–1.08; HW 1.00–1.20; EL 0.26–0.29; PW 0.79–1.03; PeW 0.43–0.57; PpW 0.50–0.64; HBaL 0.31–0.40; HBaW 0.09–0.12; CI 106.4–111.0; PI 115.8–126.6; PPeI 180.7–190.0; PPpI 158.0–166.7; HBaI 27.8–30.0.

S o l d i e r (Fig. 384 D) (description of KEMPF, 1958 a). - "Total length 5.0–5.2 mm; maximum length of head 1.53–1. 57 mm; maximum length of thorax 1.43–1.46 mm. Black; light color as in worker except for the head, which is completely black.

Head opaque, surmounted by a broadly oval, completely rimmed, excavate disc, the posterior end being narrower. Border of disc not as sharp as in *pallens* and *varians*. Floor of disc with a median convexity, slightly in front of the center, which is invisible, when head is seen in profile. Supramandibular excision obsolete, indicated by a longitudinal slit. Occipital lobes bluntly angulate. Occipital portion of disc not overhanging the more or less perpendicularly truncated occiput. Floor of disc more or less reticulate-rugose and coarsely foveolate, the foveolae on disc being unequal in size. Lower face of head rather shiny and longitudinally rugose.

Thorax opaque. Anterior border convex mesially, slightly concave laterally, mesad of the prominent lateral tooth. Transverse pronotal carina feebly developed, blunt, broadly interrupted mesially. Lateral border of pronotum somewhat sinuous. Promesonotal suture present or at least vestigial. Lateral lobe of mesonotum angulate or rounded. Mesoepinotal suture impressed. Anterior corner of basal face of epinotum subdentiform, followed posteriorly by a triangular tooth and another smaller, rectangular tooth on the posterior corner. Declivous face scarcely excavated, its lateral borders marginate, not crested. The entire thorax finely and sharply punctate, the dorsum reticulate-rugose and foveolate, the sides with a few fine more or less vestigial rugosities, especially on the laterotergite of the pronotum and the bottom half of the pleura.

Peduncular segments, gaster and pilosity, in general, as in worker. Gaster often more elongate. Sides of head and lateral rim of cephalic disc with rather long, clavate, dense projecting setae."

Measurements (in mm) and indices: TL 5.26–5.36; HL 1.36–1.48; HW 1.28–1.36; EL 0.31–0.32; PW 1.20–1.28; PeW 0.57; PpW 0.64–0.72; HBaL 0.40; HBaW 0.12–0.14; CI 91.9–100.0; PI 106.2–106.7; PPeI 210.5–224.6; PPpI 177.8–191.0; HBaI 30.0–35.0.

G y n e (description of KEMPF, 1958 a). - "Total length 7.1 mm; maximum length of head 1.57 mm; maximum length of thorax 2.10 mm. Resembling the soldier, except for the peculiarities of the caste.

Extensor face of tibiae more infuscated. Anterolateral gastral spots small, pale testaceous. Cephalic disc as in soldier, but flatter, less distinctly excavated, and when seen in profile, obliquely truncate above and behind, separating from the disc a narrow sickle-shaped band, which slopes toward occiput, being separated from the anterior portion of the disc by a marginate edge. Anteriormost ocellus in front of this carina, the posterior pair in the sickle-shaped area, lying in deeply excavate pits, facing laterad. (This feature is well represented in EMERY's figures, 1894, pl. 4, figs. 35 -37.) Basal face of epinotum with a short lateral and another similar tooth on the posterior corner. Sides of petiole practically unarmed. Gaster more elongate, its anterolateral spots very small. Standing hair much more abundant, rather evenly dispersed on dorsum of thorax, peduncle and gaster, and on the sides of the head. Scalelike hair instead less conspicuous, minute on gaster. Wings unknown."

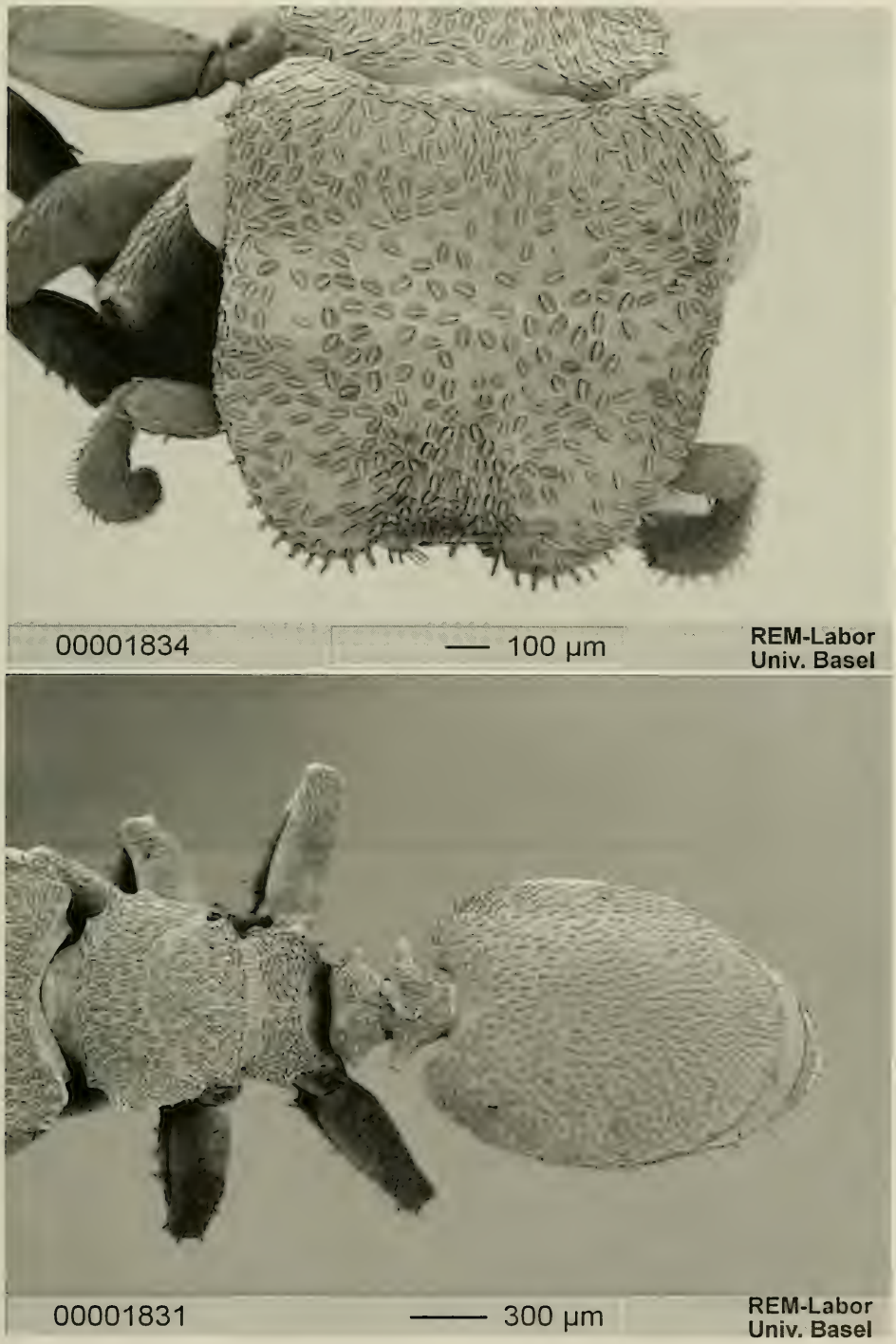


Fig. 259. *Cephalotes setulifer* (EMERY). Worker from Hamburg Farm, Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

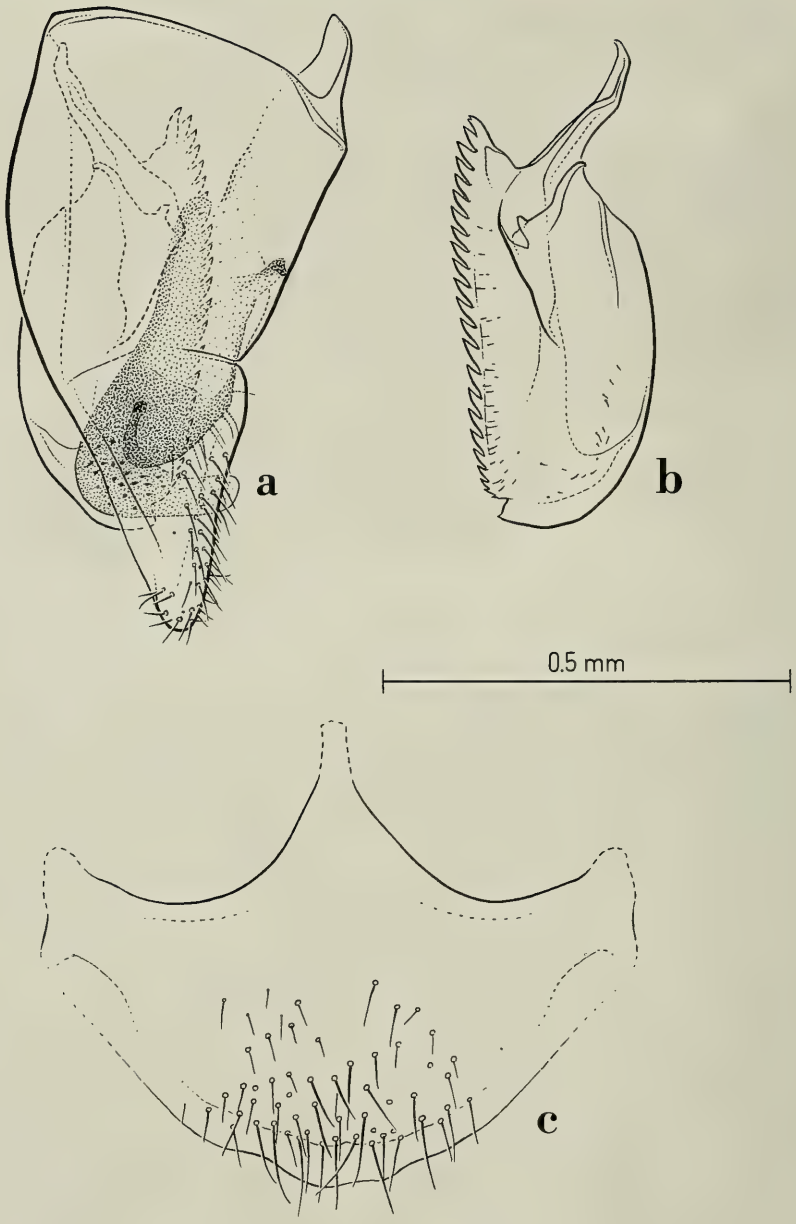


Fig. 260. *Cephalotes setulifer* (Emery). Male from Ancon, Panama Canal Zone. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Measurements (in mm) and indices: TL 6.88–7.32; HL 1.56–1.60; HW 1.32–1.36; EL 0.32; PW 1.32; PeW 0.58–0.60; PpW 0.68–0.73; HBaL 0.48; HBaW 0.16–0.17; CI 100.0; PI 100.0–103.0; PPeI 220.0–227.6; PPpI 180.8–194.1; HBaI 33.3–35.4.

M a l e (description of WHEELER, 1942). - "Length 3.8–4 mm.

Head, including the eyes, fully twice as broad as long, with a straight, broad posterior border and small rounded angles. Eyes and ocelli very convex. Mandibles very small, with very indistinctly and bluntly denticulate apical borders. Clypeus small and short, its anterior border entire and broadly rounded. Antennae very long, the scapes only one and one half times as long as broad, the remaining joints much longer than broad, diminishing in length to the penultimate which is about two-thirds as long as the last joint. Thorax broad and convex, decidedly narrower than the head; humeri of pronotum rectangular; mesonotum as long as broad, subrectangular, with well-developed Mayrian furrows dividing it into three subequal convex areas. Epinotum small and short, with subequal base and declivity, meeting at a rounded right angle. Petiole and postpetiole from above subrectangular, about as long as broad, the latter at its anterior corners with short broad teeth representing those on the corresponding segment of the other phases. Gaster slender, the first segment as long as all the remaining segments together. Legs moderately long.

Head, including the mandibles, thorax, petiole and postpetiole opaque, densely and finely punctate-rugose; gaster and legs slightly shining and merely densely punctate.

Hairs long, abundant, dull yellowish, erect, confined to the dorsal surface of the head and thorax, the tip of the gaster and flexor surfaces of the femora.

Black; antennae dark brown; tibiae and terminal tarsal joints reddish brown; genitalia and posterior borders of gastral segments golden brown or brownish yellow; wings colorless, hyaline, with pale brown pterostigma and yellowish veins."

Genitalia and subgenital plate as in Fig. 260.

Measurements (in mm) and indices: TL 5.04; HL 0.76; HW 1.04; EL 0.35; PW 1.00; PeW 0.40; PpW 0.40; HBaL 0.56; HBaW 0.07; CI 136.8; PI 104.0; PPeI 250.0; PPpI 250.0; HBaI 12.5.

M a t e r i a l e x a m i n e d . - **Costa Rica:** Jimenéz, 1 worker, 1 gyne (syntypes), A. ALFARO [MCSN]; El Hiquito near San Mateo, I.1900, 250 m, in green leaves, 1 worker, 1 soldier (syntypes of ssp. *orbis*), P. BIOLLEY [MHNG]; La Caja near San José, 06.IX.1926, 1 gyne, F. NEVERMANN [MZSP]; Hamburg Farm, Reventazón, Limón planes, 19 workers, 4 soldiers, F. NEVERMANN [MCZC, MZSP]; same locality and collector, 22.I.1938, in *Cordia alliodora*, 7 workers, 1 soldier [MZSP]; San José, 1940, 1 worker, H. SCHMIDT [MZSP]; Puerto Viejo, Heredia Prov. 30.VI.1965, 1 worker [MZSP].

Panama: Ancon, Canal Zone, on *Cordia alliodora*, 2 workers, 2 soldiers, 1 gyne, 1 male, W. M. WHEELER [MCZC, NHMB].

Colombia: R i s a r a l d a : Pereira, 100 m, V.1975, 1 worker, A. J. NEGRETT [MZSP].

D i s c u s s i o n . - *C. setulifer*, for its general habitus, is more similar to the cladistically distant *trichophorus* than to the closer *peruviensis*. It differs, however, from *trichophorus* by the shorter petiolar and postpetiolar spines, by the third pair of propodeal spines not very distant from the two anterior ones and by the first gastral sternite without longitudinal rugosities.

The workers from Ancon, Panama, differ from the others in having the body foveolation sparser.

D i s t r i b u t i o n : Costa Rica, Panama, Colombia.

Cephalotes peruviensis DE ANDRADE new species
Fig. 261

H o l o t y p e : Worker (unique) from Avispas, Peru (Madre de Dios), 400 m, 1–15.X.1962, PENA leg., MCZC.

D e r i v a t i o n o m i n i s : *peruviensis* is a neologism indicating the provenance of the species from Peru.

D i a g n o s i s . - A member of the *coffeae* clade differing from its closest species *setulifer*, *trichophorus* and *coffeae* by the frontal carinae strongly upturned over the eyes.

W o r k e r (Fig. 261). - Head gently convex in the middle, subquadrate. Frontal carinae diverging backwards, slightly converging in front and strongly upturned above the eyes; border of the frontal carinae crenulate. Vertexal angles truncate and with crenulate margin. Vertexal margin concave and continuing medially in a prominent "neck". Clypeal suture superficially impressed. Mandibles with a lateral carina.

Mesosoma almost flat in profile. Scapular angles visible in dorsal view. Pronotal sides with two pairs of short, membranaceous teeth followed by a notch and three pairs of denticles. Promesonotal suture vestigial. Mesonotum with a pair of triangular denticles with pointed tip. Propodeal suture more impressed on the sides. Propodeum superficially differentiated in basal and declivous faces; declivous face concave in the middle. Propodeal sides with one pair of broad denticles followed by two pairs of teeth, the first pair broader than the second one.

Petiole with anterior face sloping, posterior face flat to slightly concave. Petiolar sides with a pointed spine gently directed backwards. Postpetiole slightly broader than petiole; middle of the postpetiolar dorsum almost flat; postpetiolar spines broad, directed forwards and curved at the apex. Tip of the postpetiolar spines superficially crenulate.

Gaster oval. Anterolateral gastral lobes with developed membranaceous crest not surpassing the stigma backwards.

Hind femora medially angulate; mid and hind basitarsi long, slightly flattened at the base.

Sculpture. Head dorsum superficially reticulate and covered by foveae slightly broader than their interspaces, the same sculpture but sparser on the frontal carinae. Ventral face of the head reticulate and with sparse, superficial foveae smaller than those on the head dorsum. Mesosoma with the same type of sculpture as the head dorsum but the foveae are broader than their interspaces and superimposed by few, irregular, faint rugulosities. Middle of the declivous face of the propodeum reticulate. Pleurae reticulate, with longitudinal rugae ending at the beginning of the metapleurae and with small foveae on the ventral part of the meso- and metapleurae. Petiole, postpetiole, extensor face of femora and tibiae and anterior third of the first gastral tergite reticulate-foveolate, with foveae smaller and shallower than those on the mesosoma. Anterior and posterior faces of the legs and remaining gastral segments strongly reticulate and with sparse, small piligerous foveae. First half of the first gastral tergite with superficial, longitudinal rugulosities. Middle of the posterior half of the first gastral sternite shining.

Pilosity. Each fovea with an appressed canaliculate hair. Mandibles, border of the head, of the mesosoma, of the pedicel, of the gaster and whole legs with sparse, suberect, canaliculate hairs. Apex of the tergites and sternites with two types of erect hairs: (1) short, sparse and slightly canaliculate, (2) long, rare and pointed.

Colour. Basically dark brown. Frontal carinae, mesosoma and peduncular spines, apex of femora, outer face of the tibiae and tarsomeres yellowish. First gastral tergite with a pair of yellow spots anterolaterally.

Measurements (in mm) and indices: TL 4.32; HL 1.00; HW 1.20; EL 0.30; PW 0.92; PeW 0.50; PpW 0.54; HBaL 0.40; HBaW 0.10; CI 120.0; PI 130.4; PPeI 184.0; PPpI 170.4; HBaI 25.0.

M a t e r i a l e x a m i n e d . – **Peru**: M a d r e d e D i o s : Avispas, 01–15.X.62, 1 worker (holotype), PEÑA [MCZC].

D i s c u s s i o n . - For its general habitus *peruviensis* appears to be closest to the Colombian *coffeae*. The two species differ nonetheless in the following characters: anterolateral expansions of the first gastral tergite with a lamella broad in *peruviensis* vs. narrow in *coffeae*, first gastral tergite with longitudinal rugosities in *coffeae* vs. reticulate in *peruviensis* and body with foveae sparser in *peruviensis* than in *coffeae*.

D i s t r i b u t i o n : Peru.

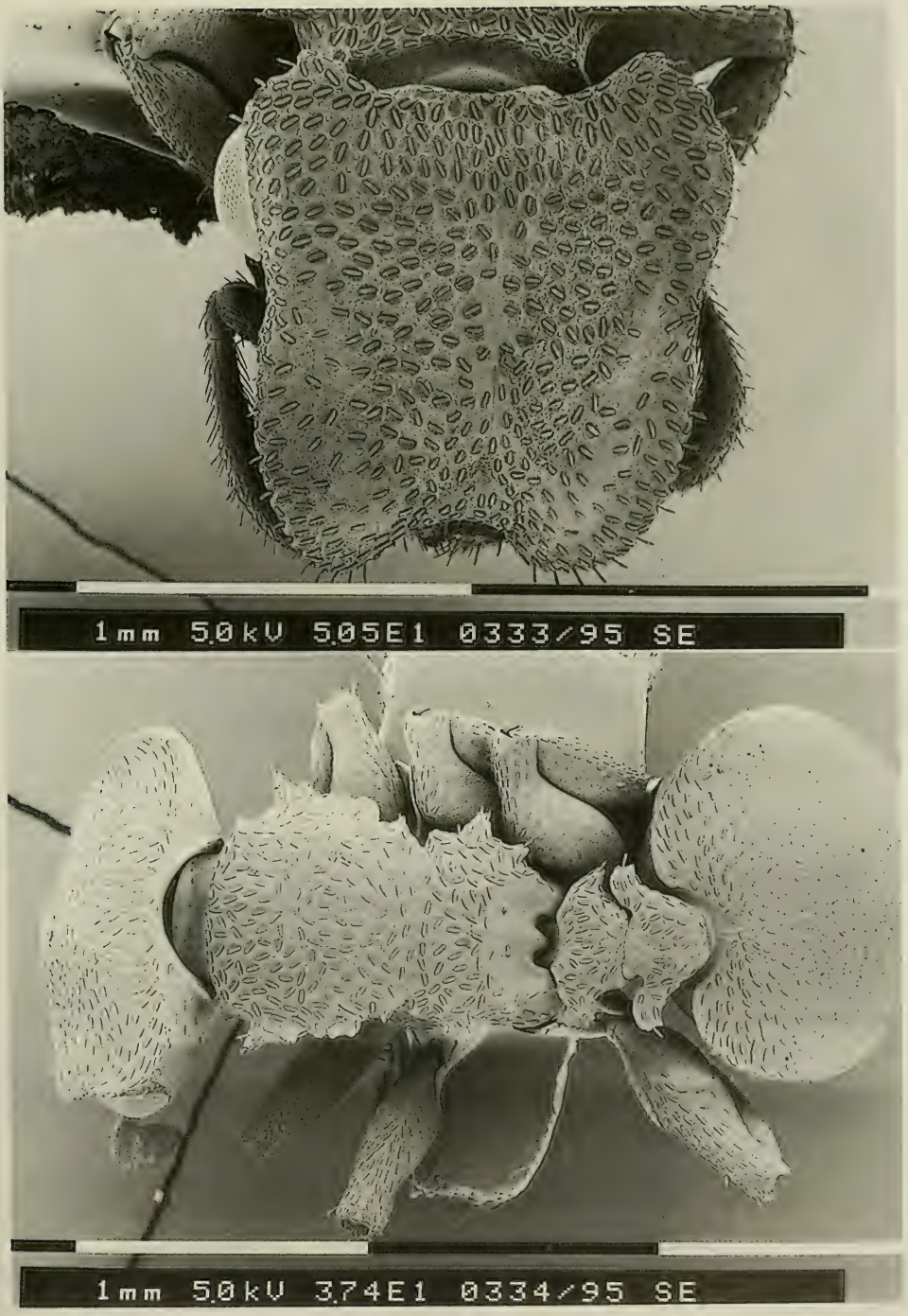


Fig. 261. *Cephalotes peruviensis* DE ANDRADE. Worker from Avispas, Peru: head (top) and meso- and metasoma (bottom) in dorsal view.

Cephalotes trichophorus DE ANDRADE new species
Fig. 262

Type material: Holotype worker from Peru labelled: Madre de Dios: Cuzco Amazónico: 15 km NE of Puerto Maldonado, J. E. Tobin & S. P. Cover, VI–27–91 [MCZC].

Derivatio nominis: *trichophorus* (i. e. bearing hairs) is composed by the two ancient Greek words θρίξ (= hair) and φέρειν (= to bear) and it has a similar meaning as the Latin *setulifer*, the name of one of its closest species.

Diagnosis.- A member of the *coffeae* clade differing from its sister species, *coffeae*, by the propodeal teeth smaller and with a broad space between the second and the third pair, and by the CI ≤ 106.

Worker (Fig. 262). - Head slightly broader than long. Frontal carinae with strongly crenulate margin, straight over the eyes. Vertexal angles subtriangular and with crenulate border. Vertex without denticles. Vertexal margin concave. Mandibles laterally carinate.

Mesosoma. Scapular angles visible. Pronotal sides with a narrow, long, subdenticulate lamella. Promesonotal suture superficially impressed. Mesonotum with a pair of small denticles. Propodeal suture impressed. Propodeum with differentiate basal and declivous faces; propodeal sides with three pairs of small denticles, the third pair on the declivous face and dis-tant from the two anterior pairs. Declivous face of the propodeum deeply concave.

Petiole slightly narrower than the postpetiole. Anterior face of the petiole truncate and superficially concave medially; petiolar sides with a pointed tooth. Postpetiole flat; postpetiolar sides with a broad expansion strongly directed anterolaterally and with crenulate apex.

Gaster suboval and with a pair of thick, narrow, anterolateral lamellae

Fore coxae angulate. Mid and hind femora angulate. Mid and hind basitarsi flat and with parallel sides.

Sculpture. Head dorsum and most of the mesosoma minutely punctate and with dense foveae, shallower and sparser on the frontal carinae, absent on the propodeal concavity. Ventral face of the head punctate, with sparse and very shallow foveae on the anterior part. Pleurae punctate, longitudinally rugose and with small foveae on the lower part. Pedicel punctate and with superficial, slightly oval foveae. First gastral tergite reticulate; its anterior third and sides with superficial, oval foveae separate by irregular, longitudinal rugosities. Remaining gastral tergites and sternites punctate and superficially shining. First gastral sternite with additional, longitudinal rugosities on the anterior third and on the sides. Legs reticulate and with superficial, oval foveae more impressed on the distal part of the femora and on the outer face of the tibiae.

Pilosity. Each fovea with an appressed canaliculate hair; similar hairs but not originating from foveae and thinner on the first gastral tergite and on the legs. Margin of the frontal carinae, vertexal angles, mesosoma, apex of the peduncular spines, first gastral tergite, and legs with thick, clubbed hairs, slightly longer on the first gastral tergite. Gastral sternites with three types of hairs: (1) long and pointed on the whole sternites; (2) appressed and thin on the first sternite; (3) erect and truncate on the posterior border of the sternites. The hairs of type (3) are also present on the terminal tergites

Colour. Black. Frontal carinae, tibiae. and tarsi brown. First gastral tergite anterolaterally with a pair of dark ferruginous or brown spots.

Measurements (in mm) and indices: TL 3.18; HL 0.82 HW 0.85–0.87; EL 0.26; PW 0.76–0.77; PeW 0.47–0.49; PpW 0.51–0.53; HBaL 0.24; HBaW 0.06; CI 103.6–106.1; PI 11.8–113.0; PPeI 155.1–163.8; PPpI 143.4–151.0; HBaI 25.0.

Material examined. - **Brazil**: Amazonas: Reserva Ducke, 21.VIII.1991, 1 worker, J. ADIS et al. [INPA].

Peru: Madre de Dios: Cuzco Amazónico, 15 km NE of Puerto Maldonado, 27.VI.1991, 1 worker (holotype), J. E. TOBIN & S. P. COVER [MCZC].

Fig. 262. *Cephalotes trichophorus* DE ANDRADE. Worker from Manaus, Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Discussion. - Both known specimens of *trichophorus* have been collected during canopy fumigation.

Distribution: Brazil and Peru.

Cephalotes coffeae (KEMPF) new combination

Paracryptocerus coffeae KEMPF, 1953: 79, figs. 1–11. Worker, soldier, gyne and male. Original description. Type locality: Tibacy (Cundinamarca, Colombia). Type material: holotype worker (MZSP), 11 paratype workers (MZSP), 2 paratype workers (MCZC), 2 paratype soldiers (MZSP), 2 paratype gynes (MZSP), 1 paratype gyne (MCZC), 1 paratype male (MZSP), examined.

Zacryptocerus coffeae (KEMPF), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

Diagnosis.- A member of the *coffeae* clade differing from its sister species, *trichophorus*, by the larger propodeal teeth with a short space between the second and third pair, and by the CI $\geq$ 112.

Worker (description of KEMPF, 1958a). - "Total length 3.9–4.7 mm; maximum length of head 1.09–1.24 mm; interocular width 1.09–1.24 mm, maximum length of thorax 1.12–1.28 mm. Black; the following ferruginous: tip of mandibles, scapes, thoracic and peduncular teeth, the tibiae and tarsites; frontal carinae testaceous with their edge light ferruginous; funicular segments fuscous-brown, becoming darker toward apex of funiculus; anterolateral gastral lobes with a light spot, light brown or ferruginous.

Head subopaque; quadrate, the interocular width always equal to the maximum length of head. Clypeal sutures vestigial. Lateral borders of head diverging very little caudad, straight, not emarginate in front of, nor noticeably upturned above, eyes. Occipital corners obliquely truncate with slightly crenulate border. Occipital border gently emarginate between the lobes. Upper face of head scarcely, but evenly convex, finely reticulate punctate, more coarsely reticulate-rugose and foveolate. Lower face of head identically, but much more superficially sculptured, rather shiny.

Thorax subopaque. Anterior border gently arcuate. Shoulders rectangular. Lateral borders of pronotum with two triangular teeth in front, followed by a more or less crenate border, the posterior corner rectangular. Promesonotal suture obsolete. Mesonotum, on each side, with a pointed, projecting tooth. Mesoepinotal suture mostly vestigial, usually fading out in the middle. Lateral border of basal face of epinotum with a subrectangular tooth on the anterior corner, followed behind by a large, triangular and somewhat foliaceous tooth, which again is followed by another similar, yet smaller tooth. Declivous face somewhat differentiated from basal face, its borders marginate but unarmed. Sculpture of dorsum of thorax as on head, the declivous face finely reticulate-punctate and opaque. Sides of thorax horizontally striato-rugose. Fore coxae with rugosities on the outer face. Hind femora, as seen in profile, not fusiform, but the extensor face forms a distinct angle, the vertex of which is bluntly rounded.

Peduncular segments subopaque, their dorsal face sculptured as dorsum of head and thorax. Petiole not quite as broad as postpetiole, its anterior face truncate, forming dorsolaterally on each side a small tubercle at its junction with the dorsal face. Lateral processes spinelike, gently curved and pointed at apex. Dorsum of postpetiole flat, its lateral processes long with strongly recurved tip.

Gaster subopaque, oval, rather strongly emarginate anteromesially, its anterolateral lobes rather broad, bearing anteriorly a vestigial, very narrow, foliaceous crest, which does not reach caudad to the level of the stigma of the first tergite. The latter finely reticulate-punctate, reticulate-rugose, forming elongated meshes. First sternite with fine longitudinal rugosities on the sides.

Standing hair on mandibles, funicular segments and apex of gaster. A row of short, thick setae projects from the lateral edge of the frontal carinae, which reaches back to the occipital corner. Scalelike hair very distinctive, long, canaliculate, golden, appressed, on dorsum of head, thorax, peduncle, gaster and extensor face of femora and tibiae. Finer, simple or canaliculate on lower face of head, gastral sternites and sides of the leg segments."

Measurements (in mm) and indices: TL 4.2–4.48; HL 0.96–1.00; HW 1.08–1.12; EL 0.26; PW 1.00–1.04; PeW 0.52–0.56; PpW 0.56–0.60; HBaL 0.31; HBaW 0.09; CI 112.0–112.5; PI 107.7–108.0; PPeI 185.7–192.3; PPpI 173.3–178.6; HBaI 29.0.

S o l d i e r (description of KEMPF, 1958a). - "Total length 5.3–5.4 mm; maximum length of head 1.57–1.62 mm; maximum width of head disc 1.48–1.52 mm; maximum length of thorax 1.48–1.50 mm. Black; the following fuscous-ferruginous: Mandibles, anterolateral portion of head disc; ferruginous: legs, first gastral tergite with four yellowish-brown spots, the posterior pair very small.

Head rather shiny, surmounted by an oval, deeply excavate, completely marginate disc, with its somewhat crenulate borders strongly raised, concealing the floor of the disc, when head is seen in profile. Lateral borders of cephalic disc convex, converging caudad, forming with the straight to slightly concave occipital border an obtuse angle. Clypeal sutures vestigial. Anterolateral portions of disc, above the antennal scrobes, slightly transparent, having in the middle, just in front of the center, a gently bulging convexity. Occipital lobes obliquely truncate at apex, the truncated border sharply marginate, continuing cephalad as a vestigial carina, toward the superior border of the eye, but fading out halfway before reaching it. Inferior border of cheeks not distinctly marginate. Floor of cephalic disc finely yet superficially or even only vestigially reticulate-punctate, either only coarsely foveolate, or reticulate-rugose and foveolate. Sides of head, occiput and lower face reticulate-rugose and foveolate.

Thorax somewhat shining on mesonotum, subopaque on pronotum and epinotum, opaque on sides. Pronotum much broader than mesonotum, its anterior border arcuate and convex in the middle, very slightly concave at the sides, its anterolateral corner dentate, its sides subparallel or slightly converging caudad in front of the transverse carina, strongly converging and slightly sinuate behind the carina, the latter very prominent, sharply edged and strongly raised, shallowly excised in the middle, when seen from the front. Promesonotal suture obsolete except on the sides. In profile the pronotum and mesonotum are at right angle, the vertex of which is formed by the transverse carina. Mesonotum flat, with a blunt, or obliquely truncated, projecting lobe on each side. Mesoepinotal groove deeply impressed. Basal face of epinotum gently transversely convex, its anterior corner bluntly rounded, its sides with a strong triangular, pointed tooth, followed at the posterior corner by a similar, somewhat smaller tooth, which is slightly raised, pointing laterad. Declivous face shallowly excavated, its sides marginate. Pronotum, in front of the carina, finely reticulate-punctate, coarsely and rather densely foveolate. Remaining portion of dorsum of thorax coarsely reticulate-rugose and foveolate, the rugosities highly shining. Sides of thorax and declivous face finely but sharply reticulate-punctate, with a few rugosities on the former. Coxae and femora as in worker.

Peduncolar segments and gaster as in worker, except for the posterior pair of light spots on the first gastral tergite. Anterolateral lobes of gaster sharply marginate, not crested. Pilosity as in worker, except for the following: Scalelike hair arising from the pits on cephalic disc shorter, and around the rim of the disc a row of thick, short, projecting setae, extending backward to the level of the eyes, where they continue on the sides until the occipital corner."

Measurements (in mm) and indices: TL 5.34–5.52; HL 1.38–1.40; HW 1.42–1.44; EL 0.30–0.32; PW 1.44; PeW 0.60–0.64; PpW 0.68; HBaL 0.34–0.36; HBaW 0.10–0.11; CI 102.8–102.9; PI 98.6–100.0; PPeI 225.0–240.0; PPpI 211.8; HBaI 27.8–32.3.

G y n e (description of KEMPF, 1958a). - "Total length 6.9–7.2 mm; maximum length of head 1.64–1.71 mm; maximum length of thorax 1.90–1.95 mm. Color as in soldier. The four spots on first gastral tergite are lighter and much more extensive. No light spot on shoulders. In general as in soldier, with the differences peculiar to the caste.

Cephalic disc slightly more elongate, less excavate, the lateral upturned borders not concealing in profile completely the anteromedian convexity of the floor of the disc. Posterior third of disc nearly flat, the borders scarcely raised, the posterior border not distinctly truncated but rather rounded. Ocelli very small, lying in pits which do not differ in size from the squamiferous foveolae. Posterior pair of ocelli very close to the occipital border.

Transverse pronotal carina less prominent, interrupted mesially, fading out laterally before reaching the sides of the thorax. Scutum coarsely foveolate. Scutellum reticulate-rugose and foveolate. Basal face of epinotum extremely short, with an obtuse tooth on each side, and another smaller tooth on the posterior corner. Declivous face somewhat excavate, very finely reticulate-punc-tate, almost smooth. Laterotergites of pronotum and mesopleura foveolate. Hind femora fusiform, not angulate above. Petiole with a short tooth on each side, the postpetiole with lateral processes, which are obliquely truncate. First gastral tergite much longer than thorax, nearly twice as long as broad. Only the first fourth of the first tergite bears fine rugulosities. Scalelike hair as in worker but finer and smaller. Standing hair also occurs all over the first gas-tral tergite, and sparsely, not regularly distributed, on peduncular segments, legs, and thorax. Wings infumated, with dark-brown veins, the pterostigma black. Veins in the apical field almost well developed, not quite vestigial. Fore wing, when folded over the back extending beyond the apex of the normally contracted gaster."

Measurements (in mm) and indices: TL 7.48-7.80; HL 1.46–1.48; HW 1.44; EL 0.32; PW 1.36–1.40; PeW 0.56–0.64; PpW 0.72; HBaL 0.40–0.44; HBaW 0.13; CI 97.3–98.6; PI 102.8–105.9; PPeI 212.5–250.0; PPpI 188.8–194.4; HBaI 29.5–32.5.

M a l e (translation of the description of KEMPF, 1953). - "Total length 5.7 mm; median head length 5.7 mm; length of the thorax 1.61 mm. Colour generally black; masticatory border of the mandibles, funiculi, tibiae and tarsi, apical borders of gastral sclerites, brown; genital parameres testaceous.

Head subopaque; larger than long, the distance between the eyes greater than the median length (34:32). Mandibles thin and densely punctated. Masticatory border with apical, subapical and two smaller median teeth. Clypeus convex, its anterior face raised perpendicularly behind the mandibles, its posterior face making a right angle and transversely convex. Frons with a light median impression in front of the anteromedian ocellus. Frontal carinae strongly diverging caudad, not reaching the posterior border of the eyes. Eyes large and convex, their maximum diameter slightly shorter than half of the median length of the head (14:32). Ocelli conspicuous, projecting over the vertex. Occipital angles obtuse, nearly round, superficially marked by a horizontal carina. Occipital border nearly straight. Integument finely and densely punctated and reticulated, with rare longitudinal rugae on the frons, transverse between the frons and the base of the eyes, with some of the rugae prolonging the frontal carinae. Inferior face with rugae more irregular and anastomosing. Antennae filiform, the scape twice as long as the first funicular joint (6:13). Joints 2–11 subequal in length, increasing in width towards the apex. Apical joint one and a half longer than the preceding joint. The space (?=scape) and the first article without hairs.

Thorax subopaque. Pronotum with transversal carina weak but distinct, at the level of which the sides possess an adjecting denticle. Lateral borders of the pronotum diverging caudad. Scutellum convex, with deeply impressed Mayrian furrows and faint parapsidal sutures. Epinotum unarmed with the posterior angles of the basal face rounded and carinate. Integument finely and densely punctate-reticulate, bearing on the pronotum and on the scutellum meshes formed by anastomosing rugae. Scutum with spaced rugae, more or less longitudinal in the middle. The sulci between the sclerites of the scutum and between the scutum and the scutellum crossed by minute carinae more pointed and spaced. Sides of the thorax and basal face of the epinotum with big rugae carenate and irregular. Declivous face finely punctate, with some spaced vertical carinae in the superior part.

Petiole subcylindrical, nearly as long as broad, finely punctate, the superior face and the sides with fine longitudinal rugae, and, between them, other transversal rugae forming elongate meshes. Sides with swelling little projecting and obtuse, in its anterior half. Postpetiole slightly shorter than broad with on each side, near the anterior border, a pointed and curved tooth. Sculpture of the superior face as in the petiole, but only with longitudinal rugae. Ventral face with longitudinal striae more pronounced.

Gaster fusiform, finely reticulate and relatively shining.

Head and thorax with abundant long bristles, sinuous and erect, brown-reddish in colour. Shorter hairs sparse and semidecumbent on the gaster; short and decumbent hairs on the legs. Short and fine pubescence on the articles 2–12 of the funiculus.

Wings infuscate, similar to those of the female, yet short, not reaching the tip of the gaster at rest".

Measurements (in mm) and indices: TL 5.68; HL 0.72; HW 0.92; EL 0.34; PW 0.88; PeW 0.40; PpW 0.44; HBaL 0.56; HBaW 0.08; CI 127.8; PI 104.5; PPeI 220.0; PPpI 209.1; HBaI 14.3.

Material examined. - **Colombia**: Cundinamarca, Tibacuy, 1500 m, nest in green branch of *Coffea arabica*, 13.3.1952, 1 worker, S. V. BERNEL & R. G. MENDOZA (holotype) [MZSP], 13 workers (paratypes) [MCZC, MZSP], 2 soldiers (paratypes) [MZSP], 3 gynes (paratypes) [MCZC, MZSP], 1 male (paratype) [MZSP], all with the same data as the holotype.

Discussion. - KEMPF (1958a) thought that *coffeae* had "no real close relatives" and could represent a species group for itself. His opinion is largely confirmed by our results: of the remaining 10 species of the *coffeae* clade, 9 have been described for the first time in this paper. The tenth species, *setulifer*, at the time of KEMPF, for the cephalic morphology of the soldier was (understandably) classified in another subgenus: *Cyathomyrmex*. The weak points of this classification have been already discussed in the introduction to the *pallens* clade (q. v.).

The soldiers of *coffeae* have the head partially covered by a thin layer of camouflage material.

Distribution: Colombia.

5.6.18. The *bimaculatus* clade

A clade containing only one species, *bimaculatus*, apparently characterised by only one, probably phylogenetically not very significant, synapomorphy: the bicoloured head of the soldier. This is a relatively uncommon character in *Cephalotes* present nonetheless homoplastically in all terminal species of our cladogram (clades *bruchi* to *angustus*). Although we can easily imagine that this trait must have some important mimetic function, its probably simple adaptive significance is the main reason to question its evolutionary significance. The main arguments, however, to maintain *bimaculatus* in a separate clade lie on its lack of important synapomorphies characterising all the species included in both its ingroup clades: *wheeleri* and *texanus*. The most important of these synapomorphies are the petiole and postpetiole with very thin and long lateral expansions (with small expansions in *bimaculatus*). From the members of the *wheeleri* clade, in addition, *bimaculatus* differs by missing all 6 synapomorphies characteristic of the clade (q. v.) and from the members of the *texanus* clade (q. v.) by missing 3 synapomorphies.

Cephalotes bimaculatus (SMITH) new combination
Fig. 263

Cryptocerus bimaculatus SMITH, 1860: 77. Gyne. Original description. Type locality: Mexico. Type material: holotype gyne labelled as such with the reference number 5970, without locality, in the BMNH, examined.

Cryptocerus aztecus FOREL, 1901 a: 125. Worker and soldier. Original description. Type locality: Cuernavaca (Mexico). Type material: 5 soldiers, 11 workers and 1 male from Cuernavaca (Mexico) in MHNG, NHMB, MCZC, MCSN, examined. Synonymy by R. R. SNELLING, personal communication, confirmed by our examination of the type material. New synonym.

Paracryptocerus aztecus (FOREL), KEMPF, 1958 a: 109, pl. 2, fig. 6, pl. 4, fig. 1, pl. 6, figs. 6, 13. Worker and soldier. First combination in *Paracryptocerus*.

Zacryptocerus aztecus (FOREL), HESPENHEIDE, 1986: 395.

Zacryptocerus bimaculatus, HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

D i a g n o s i s . - Unique member of its own clade characterised among all other species of *Cephalotes* for the following combination of characters; worker: propodeum with a small pair of denticles, gaster only slightly protruding anteriorly and with one pair of gastral spots; soldier and gyne: body foveae dense and irregular, cephalic disc concave, head bicoloured and gaster with only one pair of coloured spots.

W o r k e r (Fig. 263) (description of KEMPF, 1958a, sub *aztecus*). - "Total length 3.8–4.0 mm; maximum length of head 1.03–1.07 mm; maximum length of thorax 1.11–1.14 mm. Black; the following ferruginous: mandibles, tip of scape, basal and apical funicular segments, edge of frontal carinae, tip of tibiae, tarsites; rest of frontal carinae dark testaceous and semitransparent; tip of femora brown; anterolateral corners of gaster with a light spot, varying from yellow to ferruginous.

Head subopaque, strongly depressed, subquadrate, yet the maximum length distinctly exceeding the interocular width. Lateral border of the frontal carinae subparallel, not visibly excised in front of eyes. Lateral border scarcely upturned above eyes. Occipital corners obliquely truncate, the posterior border sharply marginate, gently emarginate. Eyes small, their greatest diameter less than one fourth of maximum head length. Dorsum of head finely reticulate-punctate, the macrosculpture being inbetween foveolate and reticulate-rugose and foveolate, the pits rather crowded, not deeply impressed, their diameter exceeding the width of their intervals. Lower face very finely reticulate-punctate, and not very coarsely reticulate-rugose, the rugae forming elongate meshes.

Thorax opaque, strongly depressed, its anterior border strongly arched mesially, somewhat concave laterally. Scapular angle incorporate in the sharply marginate lateral borders of pronotum, which conspicuously converge caudad and bear in front a subacute tooth, in the middle a vestigial, very obtuse tooth, forming a rectangular tooth at the posterior corner. Mesonotum with a more or less rounded lobe on each side. Promesonotal suture vestigial or obsolete. Promesonotum scarcely convex, the posterior portion of the mesonotum sloping abruptly downward to the impressed mesoepinotal suture and the epinotum which lies at a somewhat lower level than the promesonotum, when seen in profile. Anterior corner of basal face of epinotum subrectangular, not toothlike, the lateral border sharply marginate, forming a blunt, broad, scarcely projecting angle. Declivous face somewhat differentiated from basal face, its lateral border marginate. Dorsum of thorax finely and sharply reticulate-punctate, with coarse anastomosing rugosities forming a network, in the meshes of which lie the squamiferous foveolae. Declivous face of epinotum and sides of thorax finely reticulate-punctate with sparse, longitudinal (horizontal) rugosities, anastomosing on the pleura.

Peduncular segments opaque, their dorsal sculpture as that on dorsum of thorax. Petiole narrower than postpetiole, its anterior face nearly perpendicularly truncate, its sides bearing a small tooth, pointing laterad. Postpetiole with longer, rather stout anterolateral processes, the tips of which point obliquely caudad. Dorsum rather flat, lacking longitudinal ridges.

Gaster elliptical, opaque, strongly depressed, gently emarginate anteromesially, the anterolateral lobes broad, scarcely projecting, sharply marginate, lacking a transparent crest. The margination continues caudad along the lateral border, beyond the anterior half of the first tergite, which is finely reticulate-punctate, with rather fine, mostly longitudinal, rugosities. The squamiferous points not impressed. First sternites smooth and shining discad, reticulate-punctate laterad with more prominent, longitudinal rugosities on the sides.

Standing hair, as usual, confined to mandibles and tip of gaster, and a few short, thick setae, projecting from the lateral border of head, above eyes. Squamiform hair in foveae of head, thorax and peduncle silvery, canaliculate, but short and rather small. Finer, simple, almost minute on gaster and legs."

Measurements (in mm) and indices: TL 4.70–5.18; HL 1.12–1.20; HW 1.20–1.32; EL 0.32–0.34; PW 1.00–1.12; PeW 0.52–0.58; PpW 0.56–0.62; HBaL 0.40–0.44; HBaW 0.12; CI 103.4–110.0; PI 111.1–117.8; PPeI 192.3–193.1; PPpI 174.2–180.6; HBaI 27.2–30.0.

S o l d i e r (description of KEMPF, 1958a, sub *aztecus*). - "Total length 5.1–6.3 mm; maximum length of head 1.46–1. 89 mm; of thorax 1.43–1.68 mm. Black; the following

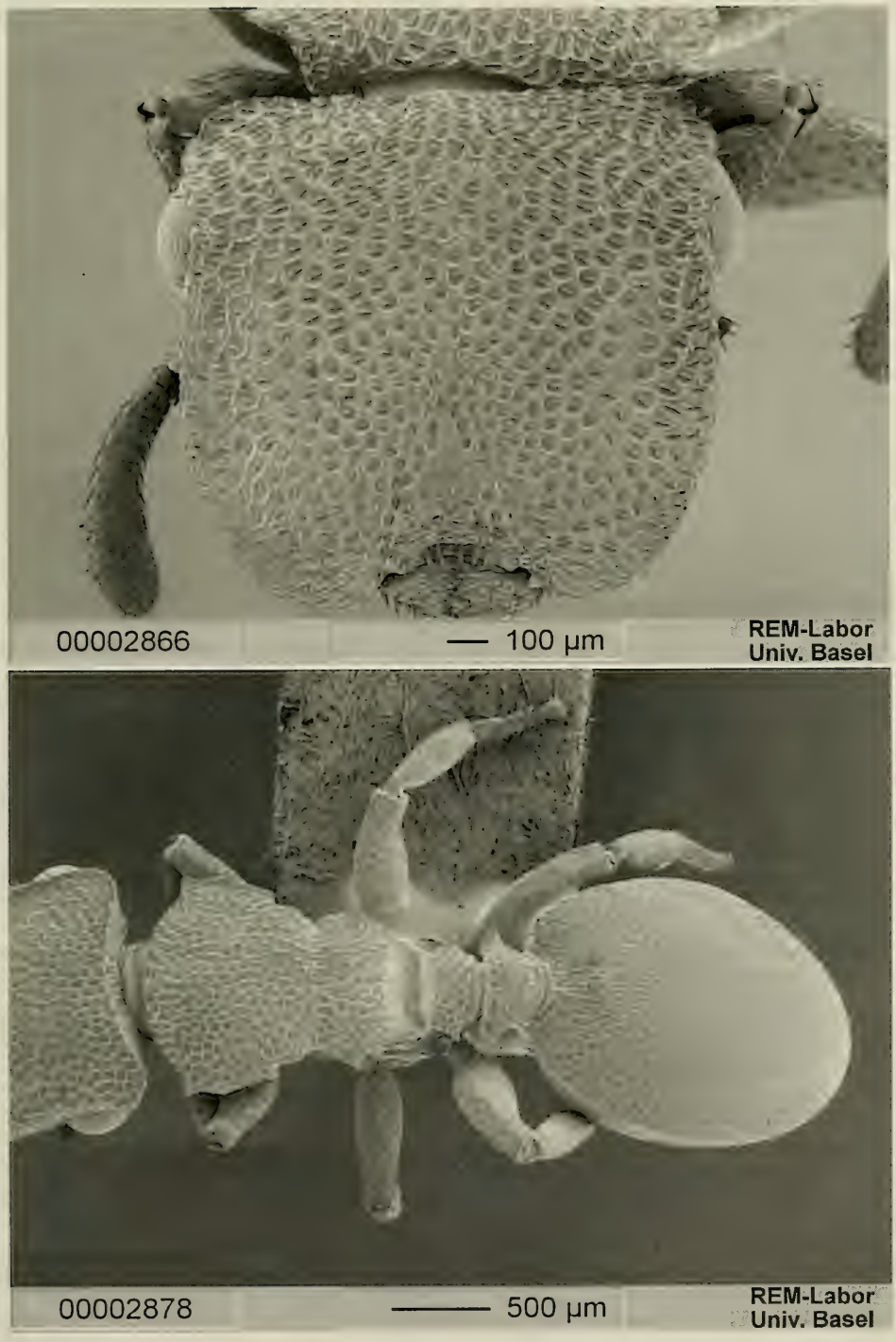


Fig. 263. *Cephalotes bimaculatus* (SMITH). Worker from Cuernavaca, Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

reddish-brown: mandibles, sides of head, occiput, pronotum in front of the transverse carina (rather infuscated), tip of femora, sides of tibiae, tarsites except the basitarsus; yellowish-brown: floor of cephalic disc, except for the anteromedian reddish-brown area, tip of scape, basal and apical funicular segments, extensor face of tibiae, and the two spots on the anterolateral lobes of gaster.

Head rather shiny, surmounted by an elliptical, elongate, excavate disc, the sides of which are strongly upturned all around, but scarcely crenulate. Floor of disc slightly raised anteromesially, just behind the vestigial clypeal area, the lateral and posterior portion of the disc excavate, not visible from the side, when head is seen in profile. Portion above frontal carinae semitransparent. Occipital lobes rectangular with their corner rounded, their borders strongly marginate posteriorly, vestigially marginate anteriorly, which in profile appears as an ascending ridge running forward toward the upper margin of eye, but fading out before reaching it. Lower border of cheeks marginate. Floor of disc and sides of head and occiput coarsely and strongly reticulate-rugose, forming more or less rounded meshes, which are deeply excavate, their bottom finely but only vestigially punctate, both ridges and pits are shining. Lower face of head with similar yet more superficial sculpture.

Thorax subopaque on dorsum, opaque on sides. Pronotum much broader than mesonotum, its anterior border gently arched, its anterolateral corner dentate, its lateral border strongly marginate, nearly straight evenly converging caudad, both in front and behind the slightly crested and raised transverse carina, which is not conspicuously interrupted mesially. Promesonotal suture present. Mesonotum on each side with a prominent, broadly truncate, oblique, strongly marginate lobe. Mesonotum flat. Mesoepinotal suture indicated by a depression in front of the transversely gently convex basal face of epinotum, the lateral border of which bears a triangular, broad little prominent projection, forming a blunt angle. Posterior angle of basal face unarmed. Declivous face of epinotum superficially reticulate-punctate, slightly excavate, somewhat shiny, its lateral border marginate. Dorsum of thorax with the same sculpture as on cephalic disc, but the bottom of the foveolae, circumscribed by the shiny ridges, is rather opaque, due to heavier microsculpture. Sides of thorax, including laterotergite, finely reticulate-punctate, irregularly rugose and reticulate-rugose. Squamiform foveolae sparse. Hind femora fusiform. Peduncolar segments and gaster as in worker, the former stouter, and the lateral processes slightly shorter. The lateral margination of the first gastral tergite is less distinct, likewise the longitudinal ridges on each side of the mesially smooth first gastral sternite. Conversely, the fine mostly longitudinal rugosities on first gastral tergite a little more prominent.

Standing hair as in worker, in addition a row of projecting, slightly clubbed setae, around the cephalic disc, excluding the posterior border, on the occipital lobes, on the sides of pronotum and a few on the tips of peduncular spines and the posterior border of the body of the postpetiole. Scalelike hair very prominent, rather long, silvery, decumbent, in the foveolae of head, thorax and peduncle, smaller on legs, minute on gaster."

Measurements (in mm) and indices: TL 6.24–6.84; HL 1.60–1.76; HW 1.68–1.76; EL 0.36; PW 1.68–1.72; PeW 0.60–0.68; PpW 0.64–0.72; HBaL 0.42–0.44; HBaW 0.14–0.16; CI 100.0–105.08; PI 100.0–102.3; PPeI 252.9–280.0; PPpI 238.9–262.5; HBaI 33.3–36.4.

G y n e . - Head disc present. Posterior two thirds of the head dorsum slightly convex, anterior third moderately flat. Frontal carinae expanded anteriorly, converging posteriorly before the beginning of the eyes, connected by a convex carina on the vertex. Vertexal angles almost round and with crenulate margin. Eyes convex, not hidden by the disc in dorsal view. Clypeal border anteriorly concave. Mandibles with a lateral carina.

Mesosoma flat in side view. Humeral angles with an obtuse tooth anteriorly, straight posteriorly. Pronotal crest marked by a thin carina, superficially interrupted in the middle. Promesonotal suture impressed. Propodeum differentiated in basal and declivous face; basal face with slightly convex dorsum and sides, with a short, broad tooth in the middle of the sides and with a sulcus in the middle of the dorsum; declivous propodeal face with sides converging posteriorly and almost straight.

Petiole with differentiated anterior and posterior faces; anterior face declivous, posterior face moderately sloping backwards and with a small, broad denticle on each side. Postpetiole

broadly convex, each side bears a broad tooth with obtuse tip arising anteriorly and prolonged backwards up to the middle of the postpetiole.

Gaster with protruding anterior border and with a superficial carina not reaching the stigma.

Legs. Fore coxae with anterior tumulus. Mid and hind femora without angle or denticles. Mid and hind basitarsi without broad base and compressed laterally.

Wings. Fore wings with *R+Sc* superficially reaching a marked pterostigma; *2r* marked, *Rsf5* connected with *R1*; distal parts of *A*, *Cu-A1* and *Mf4* vestigial. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; *CuA*, *M* and distal part of *1A* vestigial.

Sculpture. Head, mesosoma and pedicel punctate and covered by deep foveae without interspaces between them on the head dorsum and more sparse on the anterior half of the pronotum. Ventral part of the head punctate, with anastomosing longitudinal rugosities alternated with foveae. Sides of mesosoma and legs deeply punctate, with few, almost longitudinal, rugosities on pro-, meso- and lower metapleural parts, on the distal part of the mid and hind femora and on the outer face of the tibiae. Gaster and posterior half of the declivous face of the propodeum punctate. First gastral tergite with anastomosing longitudinal rugosities on the first third, thinner on the last third. First gastral sternite with anastomosing rugosities on the anterior third and on the sides, shining on the middle. Few irregular rugosities on the meso- and metapleurae. Outer face of the tibiae with oval and superficial foveae.

Pilosity. Each fovea with an appressed canaliculate hair. Rim of cephalic disc with a fringe of moderately clavate hairs. The same type of hairs but sparser on the mesosoma, on the pedicel, on the legs and on the gaster, longer and less clavate on the apex of the gaster.

Colour. Dark brown to black. Frontal carinae reddish, outer face of tibiae, articulations between femora and tibiae and tarsomeres ferruginous. Anterior third of the first gastral tergite with an orange spot on each side.

Measurements (in mm) and indices: TL 8.32; HL 1.72; HW 1.68; EL 0.38; PW 1.72; PeW 0.72; PpW 0.82; HBaL 0.60; HBaW 0.18; CI 97.7; PI 97.7; PPeI 238.9; PPpI 209.7; HBaI 30.0.

Material examined. - **Mexico**: without further locality, 1 gyne (holotype) [BMNH]. Morelos, Cuernavaca, 11 workers, 5 soldiers (syntypes of *aztecus*) [MHNG, NHMB, MCZC, MCSN]; Cuernavaca, 26.VI.1928, 1 worker [MCZC]; Cuernavaca, 22–24.VI.1929, 5 workers, 4 soldiers [MCZC, MZSP]; Cuernavaca: 3 workers, 2 soldiers [MCZC].

Discussion. - *Bimaculatus* is a very distinct species for the characters already given in the diagnosis. It has been rarely collected until now being known only from the unique holotype described from "Mexico", from the type locality of *aztecus* (Cuernavaca), and from near San Patricio, Jalisco (R. R. SNELLING personal communication).

The synonymy between *bimaculatus* SMITH and *aztecus* FOREL suggested by R. R. SNELLING (personal communication) leaves no doubt after our examination of the types of both species.

Distribution: Mexico.

5.6.19. The *wheeleri* clade

A small clade containing only 5, very distinctive, species, all restricted to a broad Sinaloan-Sonoran region from Arizona to the states of Jalisco and Morelos to the south and including Las Islas de Tres Marías. These species are easily recognisable and, in our cladogram, they are characterised by a set of six synapomorphies: for the workers, (1) the postoccipital suture extending over the ventral side of the head, (2) the first gastral tergite striate, (3) the loss of gastral coloured spots, (4) the presence of erect, truncate hairs, and, for the soldiers, (5) the antennal scrobes terminating

below the eyes, and, for the gynes, (6) loss of the gastral coloured spots (a trait not necessarily correlated with the analogous one of workers). In spite of their compact phylogenetic robustness and unequivocal presence of advanced synapomorphies (soldiers and gynes with disc, etc.), the workers of the species of this clade bear a strong, superficial similarity with the basalmost *Cephalotes* clade: the *hamulus* clade.

Species included in the clade: *hirsutus*, *insularis*, *rohweri*, *toltecus*, *wheeleri*.

Cephalotes rohweri (WHEELER) new combination
Figs. 264, 265, 266

Cryptocerus rohweri WHEELER, 1916: 32, fig. 2. Worker, soldier. Original description. Type locality: Buehman Canyon, Santa Catalina Mountains (Arizona). Type material: lectotype soldier in the U. S. National Museum, Washington, D. C., syntypes workers and soldiers in the U. S. National Museum, Washington, D. C., MCZC, MZSP (KEMPF, 1958 a: 129), examined in part.

Cryptocerus rohweri WHEELER, M. R. SMITH, 1947 a: 34. Worker, soldier, gyne.

Cryptocerus rohweri WHEELER, M. R. SMITH, 1947 b: figs. 51, 52. Worker, soldier.

Paracryptocerus rohweri (WHEELER), M. R. SMITH, 1951: 825. First combination in *Paracryptocerus*.

Paracryptocerus rohweri (WHEELER), KEMPF, 1958 a: 129, pl. 2, fig. 8, pl. 4, fig. 2, pl. 6, fig. 12.

Paracryptocerus rohweri (WHEELER), KRAFCHICK, 1959: 63, fig. 19 (penis valve), 65, fig. 9 (male ninth sternum), 69, fig. 3 (male paramere).

Cryptocerus rohweri WHEELER, SNELLING, 1968: 9, fig. 2. Worker and soldier.

Zacryptocerus rohweri (WHEELER), D. R. SMITH, 1979: 1403. First combination in *Zacryptocerus*.

Zacryptocerus rohweri, HESPENHEIDE, 1986: fig. 2. Worker.

D i a g n o s i s . - A member of the *wheeleri* clade differing from all the other species of the clade in the worker by the head and mesosoma irregularly foveolate-rugulose and by the infuscate frontal carinae, in the soldier and in the gyne by the dense foveae on the head and by the presence of hairs around the disc.

W o r k e r (Fig. 264) (description of KEMPF, 1958a). - "Total length (only one specimen measured) 5.2 mm; maximum length of head 1.28 mm; maximum length of thorax 1.43 mm. Black; the following ferruginous: mandibles, part of frontal carinae, apex of femora and tibiae, tarsites II - V.

Head opaque, trapezoidal. Occipital corners not lobate, nor obliquely truncate, forming merely an obtuse angle. Occipital border straight and transverse. Dorsal face, excepting the rather flat, posteriorly very thick and scarcely translucid frontal carinae, and the declivous clearly limited clypeus, convex, finely and sharply punctate, coarsely foveolate, the pits wanting on the frontal carinae and on the clypeus. Lower face coarsely reticulate-rugose and foveolate.

Thorax opaque. Anterior border convex in the middle, slightly concave toward the sides. Scapular angle incorporated in the lateral pronotal crest, the latter tridentate, the anterior two teeth close together, triangular, the third tooth, forming the posterior corner of the crest, subrectangular. Promesonotal suture absent. Sides of mesonotum unarmed, immarginate. Mesoepinotal suture absent. Each side of epinotum with a slender spine, pointing laterad and slightly upward and caudad. In profile the dorsum of the thorax noticeably sloping behind pronotum, the latter convex and ascending. The entire thorax sharply punctate. Dorsum reticulate-rugose, the meshes elongate on mesonotum. Declivous face with longitudinal striae. Laterotergite of pronotum reticulate-rugose and foveolate. Pleura longitudinally rugose.

Peduncular segments opaque, their dorsal face mostly longitudinally rugose. Body of petiole subglobose, its anterior face vertically truncate; from each side of the petiole at some distance from the anterior border, arises a slender, log, slightly curved and pointed spine, pointing obliquely caudad and upward. Postpetiole with anteriorly broad, posteriorly more

constricted body. A slender, longer, more recurved and pointed spine arising from each side, next to the anterior border. Dorsum of postpetiole, as seen in profile, nearly flat.

Gaster oval, opaque, finely and sharply punctured throughout. Postpetiole insertion not emarginate, anterolateral borders immarginate. First tergite finely and densely longitudinally rugose on the sides.

Standing hairs pointed, short, sparingly scattered over dorsum of head, thorax, peduncle and gaster, also on sternites, more oblique, but not decumbent, on legs. Silvery scalelike hair minute on posterior portions of head disc, larger and more conspicuous on cheeks, dorsum of thorax, laterotergite of pronotum, dorsum of peduncular segments, lacking on gaster, but present on apical half of extensor face of femora. All foveolae on dorsum of head bear a small decumbent hair, visible only under high magnification."

Measurements (in mm) and indices: TL 4.04–5.54; HL 0.96–1.28; HW 1.04–1.36; EL 0.26–0.35; PW 0.92–1.22; PeW 0.46–0.60; PpW 0.55–0.65; HBaL 0.44–0.56; HBaW 0.09–0.12; CI 106.2–111.6; PI 111.5–115.5; PPeI 192.8–214.0; PPpI 167.3–192.8; HBaI 19.2–21.4.

S o l d i e r (Fig. 265) (description of KEMPF, 1958a). - "Total length (one specimen only measured) 6.9 mm; maximum length of head 1.85 mm; maximum length of thorax 1.82 mm. Black; the following fuscous-ferruginous: anterolateral portions of head (variable in extent, always much infuscated), extreme tip of last funicular segment, knees and tarsites II - V.

Head supopaque, surmounted by a slightly elongate disc (52:47), the borders of which are evenly rounded anteriorly, except for the supramandibular excision, subparallel and rather straight on the sides, then abruptly, yet not forming a sharp angle, curved mesad, to join the scarcely convex, subtruncate occipital border. Floor of disc moderately excavated anteriorly, shallowly excavated laterally, scarcely behind, having in the center a little prominent convexity. Occipital lobes subrectangular. Clypeal sutures obsolete. Lateral border of lower face of head not distinctly marginate. Integument of head finely reticulate-punctate, more superficially and densely on dorsum, more coarsely on lower face. Likewise densely covered with large, rounded foveolae, the intervals between the foveolae not as broad as the diameter of the pits.

Thorax opaque. Anterior border convex in the middle, slightly concave toward the sides. Anterior corner sharply dentate, the lateral border of the pronotum subparallel and crenulate in front of the carina, converging, rather straight behind the carina, not forming a prominent corner when joining the mesonotum. Transverse carina sharply marginate and somewhat crenulate, broadly yet shallowly excised in the middle. Promesonotal suture vestigial. Lateral lobes of mesonotum scarcely projecting, broad, rounded, immarginate. Mesoepinotal suture distinct. Anterior and posterior corner of basal face of epinotum rounded, not angulate. On each side, somewhat in front of the posterior corner, a strong, prominent spine, pointing mainly laterad. Sculpture of thorax as that of head, the foveolae sparser, except on basal face of epinotum. Bottom of foveolae rather shiny. Foveolae very sparse and irregularly dispersed on sides of the thorax, which also present reticulate rugosities. Declivous face without macrosculpture.

Peduncular segments opaque, dorsally reticulate-rugose and foveolate, their shape and lateral processes as in worker, but their bodies are more transverse, broader, and the spines are shorter. Postpetiole much broader than petiole.

Gaster dorsally opaque, ventrally more shining. Postpetiolar insertion very little emarginate. Anterolateral borders of gaster immarginate, never crested. First tergite heavily and densely punctate, with fine, longitudinal, dense rugosities, fading out caudad, before reaching the half. Sculpture of sternite identical but more superficial.

Standing hairs long and pointed at tip around the rim of cephalic disc anterolaterally, shorter and sparingly on dorsum of thorax, peduncle, and gaster, and on the sternites. Oblique on legs. Decumbent hair in foveolae of head and thorax usually very fine and scarcely visible, scalelike, silvery and glittering only on posterior border of basal face of epinotum, on peduncular segments, none on legs and gaster."

Measurements (in mm) and indices: TL 6.82–7.44; HL 1.60–1.72; HW 1.72–1.84; EL 0.36; PW 1.68–1.88; PeW 0.62–0.72; PpW 0.76–0.88; HBaL 0.48–0.57; HBaW 0.12–0.16; CI 106.9–109.5; PI 97.8–102.4; PPeI 255.5–272.5; PPpI 209.1–223.8; HBaI 24.5–28.6.

Fig. 264. *Cephalotes rohweri* (WHEELER). Worker from Peña Blanca Springs, Arizona: head (top) and meso- and metasoma (bottom) in dorsal view.

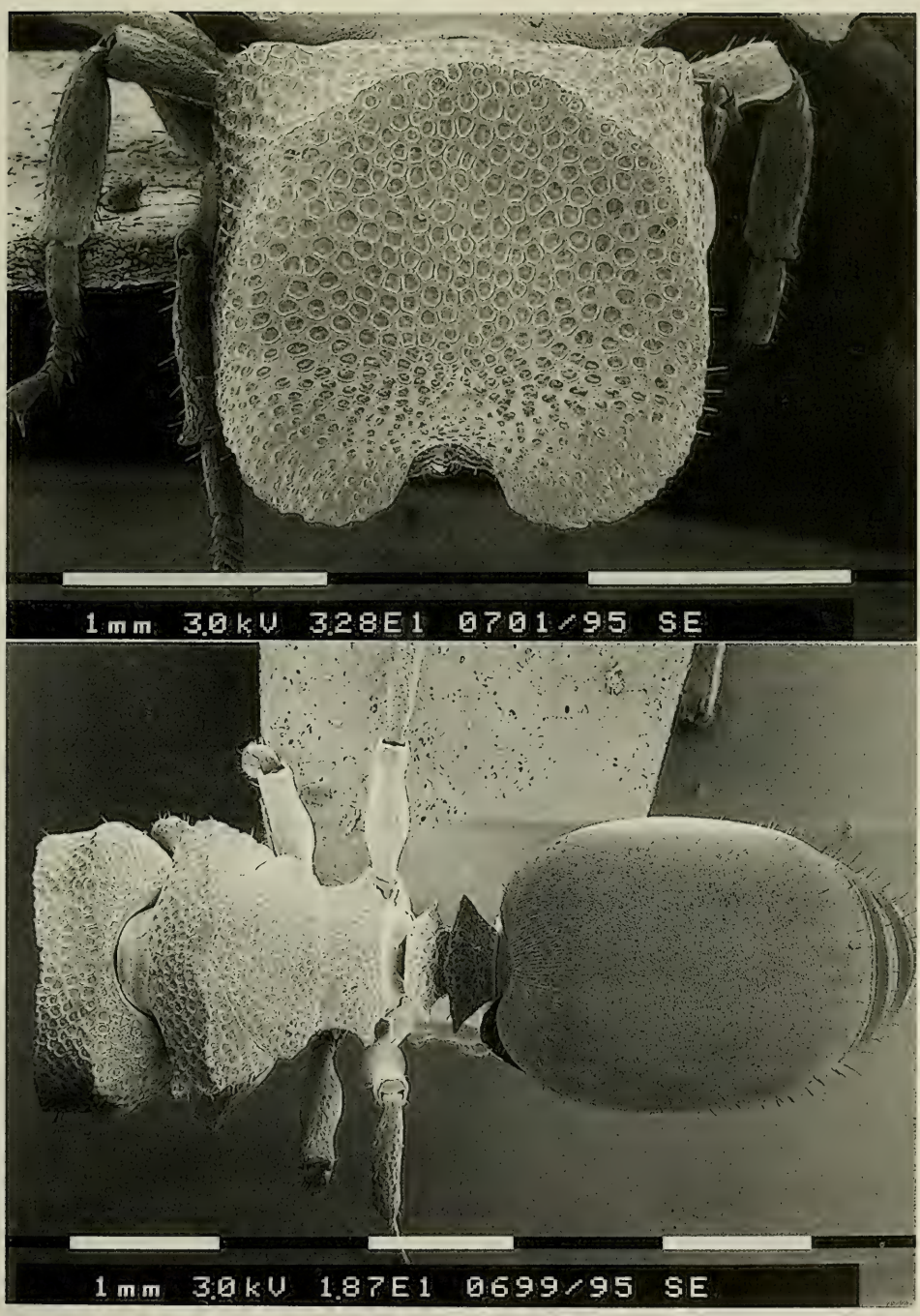


Fig. 265. *Cephalotes rohweri* (WHEELER). Soldier from Peña Blanca Springs, Arizona: head (top) and meso- and metasoma (bottom) in dorsal view.

G y n e (Fig. 266). - Head disc present. Posterior two thirds of the head dorsum almost flat, with a broad, little protruding central tumulus. Anterior third of the head moderately concave. Frontal carinae broadly expanded anteriorly, converging posteriorly and connected by a convex carina on the vertex. Vertexal angles round and crenulate. Eyes convex and not hidden by the disc in dorsal view. Anterior clypeal border concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma flat in side view. Humeral angles with an obtuse tooth anteriorly, straight posteriorly. Pronotal carina marked and superficially interrupted in the middle. Promesonotal suture impressed. Propodeum differentiated in basal and declivous face; basal face weakly convex dorsally, with convex sides; declivous face little concave on the middle.

Petiole distinctly differentiated in anterior and posterior faces; anterior face vertical, posterior face slightly convex and with unarmed sides. Postpetiole broadly convex, with a small lateral denticle on one side only of the sole available specimen.

Gaster without lateral margin, with protruding anterior border.

Legs. Fore coxae with anterior tumulus. Mid and hind femora without angle or denticles. Mid and hind basitarsi without broad base and not compressed laterally.

Sculpture. Head, mesosoma and pedicel deeply punctate and covered by deep foveae broader than their interspaces, suboval and denser on the pedicel. Frontal carinae punctate and with foveae sparser, smaller and shallower than in the other parts of the head. Sides of the fore femora, ventral part of the mesopleurae and dorsal part of the metapleurae punctate, with superficial and sparse foveae. Posterior half of the declivous face of the propodeum, legs and gaster reticulate-punctate, the same structure is present but very superficial on the ventral part of the first gastral sternite which is shining. Outer face of the tibiae with oval and superficial foveae. Anterior fourth of the first gastral tergite and sides of the anterior half of the first gastral sternite with anastomosing rugosities and rare foveae. Few irregular rugosities on the meso- and metapleurae.

Pilosity and colour as in the soldier.

Measurements (in mm) and indices: TL 7.92–8.24; HL 1.60–1.64; HW 1.64–1.72; EL 0.36; PW 1.60–1.68; PeW 0.55–0.56; PpW 0.66–0.78; HBaL 0.64; HBaW 0.14; CI 102.5–104.9; PI 102.4–102.5; PPeI 285.7–305.4; PPpI 205.1–254.5; HBaI 21.9.

M a l e . - We did not see males of this species although they are likely to be represented in some collection. There is no formal description of this sex in the literature, except for the drawings of the genitals given by KRAFCHICK (1959). These drawings are based on material presumably preserved in the USNM and are accompanied by the following descriptive remarks deduced from the key and referred to both *rohweri* and *texanus*:

„Basal ring entire. Paramere with the distal end rounded and ventral margins entire; notches, hooks, projections absent. Anterior ventral corner of paramere rounded or with a small point. Anterior margin of the IX sternum pointed or rounded. Point absent from corner of volsellar lobe. IX sternum with the lateral and mesal apodemes simple. Digitus a short and broad hook. Penis valve longer than wide."

M a t e r i a l e x a m i n e d . - **United States**: A r i z o n a : Tucson, Catalina Foothills, 30.XII.1962, 3000', in *Cercidium microphyllum*, 29 workers, 2 soldiers, 3 gynes, W. S. CREIGHTON [LACM, MCZ]; Tucson, 13.VIII.1936, 25.VI, 09.VII and 26.VIII.1937, 10 workers, 1 soldier, 2 gynes, J. N. KNULL [LACM]; Ruby, 14.VII.1952, 1 gyne, D. J. & J. N. KNULL [LACM]; Sabino Can. 04.VI.1951, 1 worker, D. J. & J. N. KNULL [LACM]; Sabino Canyon, Sta. Catalina Mts. 29.VII.1945, 1 worker, 1 soldier, 1 gyne, E. D. ALGERT [LACM]; Forestry Cabin, Baboquivari Mts. 29.VII.1951, 10.IV.1963, in mesquite, 3,500', 4 workers, 2 soldiers, 1 gyne, W. S. CREIGHTON [LACM]; Buehman Canyon, Santa Catalina Mountains, in *Cercidium torreyanum*, Hopkins, no. 10193, 3 workers (syntypes) [LACM, MCZ, MZSP], same locality, 1 soldier (labelled as lectotype probably by Kempf but contradicting the lectotype designation of KEMPF, 1958 a) [MCZC], same locality, 1 soldier, M. Chrisman (syntype) [MZSP]; Peña Blanca Sprs., Sta. Cruz Co., 07.XI.1952, in *Quercus emoryi*, 3,700', 8 workers, 3 soldiers, 1 gyne, W. S. CREIGTHON [LACM].

Mexico: S o n o r a : 13.6 mi. W Alamos, 17.VII.1963, 1 gyne, R. L. WESTCOTT [LACM]; Alamos, 29.VI.1976, 2 workers, A. MINTZER [LACM]; San Carlos Bay, 4.IV.1966,

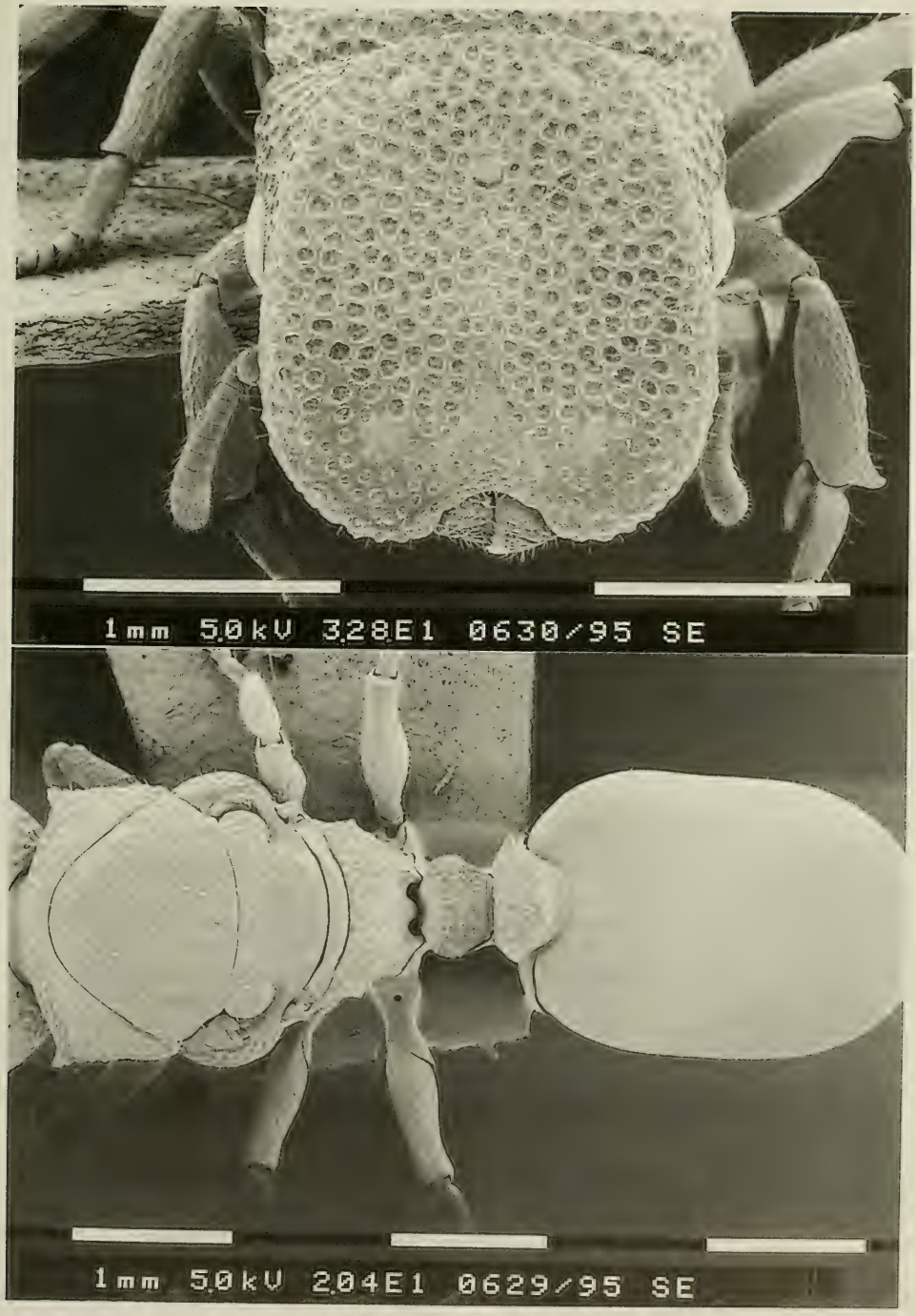


Fig. 266. *Cephalotes rohweri* (WHEELER). Gyne from Peña Blanca Springs, Arizona: head (top) and meso- and metasoma (bottom) in dorsal view.

1 worker, G. R. BALMER [LACM]; El Desemboque, 23–24.IX.1973, 1 worker, V. ROTH & W. BROWN [LACM]; vic. Punta San Antonio, 7 mi. WSW Bahia San Carlos, 8.IV.1968, Ex. *Viscainoa geniculata*, 1 small soldier, E. M. FISCHER [LACM]. S i n a l o a : El Carrizo, 3.1 mi S, 200', 10.III.1969, 5 workers, R. R. SNELLING [LACM].

D i s c u s s i o n . - *C. rohweri* is the most collected species of the *wheeleri* clade. All the female castes of *rohweri* can be easily distinguished from the other species of the *wheeleri* clade by means of the strong body reticulation. Most of the *rohweri* workers we examined have the frontal carinae infuscate instead of semi-transparent as in the other species of the clade. The soldier and the gyne of *rohweri* are also characteristic for having the border of the cephalic disc with a fringe of projecting setae.

SNELLING (1968) recorded *rohweri* from Mexico on the base of a single gyne. We had the opportunity to examine more Mexican material differing from the Arizonan specimens in the following characters: 7 out of 9 workers have reddish, semi-transparent frontal carinae and reddish legs. The gyne from Alamos, Sonora, differs from the other gynes of *rohweri* we saw for the head much broader than the maximum pronotal width (HW 1.76, PW 1.64 in the Alamos gyne vs. HW 1.64–1.72, PW 1.60–1.68 in other gynes); in addition, the gyne from Alamos differs from those of *rohweri* in microsculpture: the body reticulation is less impressed, the foveae on the disc are smaller and more regular, the frontal carinae are reddish anteriorly.

D i s t r i b u t i o n : Arizona and Mexico.

Cephalotes wheeleri (FOREL) new combination
Figs. 267, 268

Cryptocerus wheeleri FOREL, 1901 a: 126. Worker, soldier. Original description. Type locality: Cuernavaca (Morelos, Mexico). Type material: lectotype soldier in MZSP and several paralectotype workers and soldiers divided between the MCZC, MHNG, MZSP, MCSN and USNM (KEMPF, 1958 a: 132), examined.

Paracryptocerus wheeleri (FOREL), WHEELER & WHEELER, 1954 b: 157, figs. 39, 40. Larva. First combination in *Paracryptocerus*.

Paracryptocerus wheeleri (FOREL), KEMPF, 1958 a: 132, pl. 8, figs. 1, 2. Worker, soldier.

Cryptocerus wheeleri FOREL, SNELLING, 1968: 9, fig. 2. Worker and soldier.

Zacryptocerus wheeleri, HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *wheeleri* clade differing from its sister species, *toltecus*, in the worker by the genal area and the mesosoma with more regular longitudinal rugosities, and, in the soldier, by the disc with sparser foveae and without short, broad, medial tumulus.

W o r k e r (Fig. 267). - Vertexal angles rounded, with superficially crenulate borders. Occiput almost straight. Postoccipital suture open antero-ventrally. Cheeks not marginate. Frontal carinae with a notch over the eyes. Antennal scrobes reaching the antero-ventral border of the eyes posteriorly. Anterior clypeal border concave. Mandibles laterally superficially carinate.

Mesosoma convex in side view. Pronotum in dorsal view with the anterior border convex. Scapular angles absent or not visible in dorsal view. Pronotal sides with narrow lamellae bearing three teeth. Humeral angles with a short, pointed, lateral teeth slightly bent anteriorly, followed by another tooth of the same size or smaller than the first and variably pointed, and by a third broad and obtuse tooth. Sides of the mesonotum converging and unarmed. Promesonotal and propodeal sutures superficially marked in some specimens, better visible

on the sides. Propodeum declivous, without distinct, differentiate, basal and declivous faces, with a pointed, thin spine at the end of its first half, directed laterally and slightly upwards.

Petiole anteriorly truncate; its anterior border marked by a transversal carina variably impressed. Petiolar spines half of the length of the petiole, thin, pointed backwards and placed on the middle of the petiolar sides. Postpetiole broader than petiole, with thin, pointed spines arising anterolaterally and curved backwards at the base.

Gaster oval, without crest or lateral margin.

Hind and mid femora neither angulate nor denticulate; mid and hind basitarsi long and without flat and broad base.

Sculpture. Head dorsum reticulate and with superficial, slightly irregular foveae sometimes sparser behind the clypeus, denser on the vertexal angles. Frontal carinae superficially punctate. Ventral face of the head and sides of the mesosoma striato-rugose, superficially reticulate, slightly shining. Mesosoma and pedicel minutely reticulate, striato-rugose and with few, irregular foveae. Gaster superficially reticulate and shining. First gastral tergite with longitudinal rugulations originating from the articulation with the postpetiole and diverging backwards. First sternite with longitudinal rugulations on the sides only. Legs minutely reticulate-punctate, with slightly shining femora. Distal part of the mid and hind femora and outer face of the tibiae with irregular, superficial foveae and rugosities.

Pilosity. Body with three types of sparse hairs: (1) long, erect, truncate, on the mesosoma, on the pedicel and gaster, slightly shorter on the head dorsum; (2) appressed and thick, denser on the occipital borders, on the dorsal sides of the mesosoma and on the pedicel, shorter and thinner on the frons, on the middle of the mesosoma and posterior border of the first gastral tergite and legs; (3) minute and thin on the gaster and on the legs.

Colour. Dark brown to black, with yellowish frontal carinae, reddish-brown antennae and femora, lighter tibiae, tarsi, propodeal and peduncular spines.

Measurements (in mm) and indices: TL 3.84–4.28; HL 0.92–1.04; HW 1.04–1.20; EL 0.28; PW 0.84–0.98; PeW 0.48–0.56; PpW 0.56–0.60; HBaL 0.40–0.48; HBaW 0.08–0.09; CI 113.0–115.4; PI 122.4–123.8; PPeI 175.0; PPpI 150.0–163.3; HBaI 18.7–20.0.

S o l d i e r (Fig. 268). - Head disc present. Head dorsum with the anterior third declivous and concave on its sides, the rest flat and slightly lower than the borders of the disc. Frontal carinae broadly expanded anteriorly, converging posteriorly and connected by a convex carina on the vertex. Vertexal border round and marginate on the sides. Eyes moderately flat and not hidden by the disc. Clypeal border deeply concave anteriorly. Mandibles laterally carinate and partially hidden by the frontal carinae.

Mesosoma. Humeral angles with a broad, obtuse tooth anteriorly, their sides converging posteriorly. Pronotal carina marked on the sides but discontinuous in the middle. Promesonotal suture impressed. Mesonotal sides with a broad tooth with pointed tip, rarely obtuse. Lower mesopleurae without denticles. Propodeum differentiated in basal and declivous faces; basal face slightly convex dorsally, with a pointed tooth in the middle of each side and converging posteriorly to the declivous face; declivous face concave in the middle.

Petiole with distinctly differentiated anterior and posterior faces; anterior face vertical, posterior face slightly convex and bearing a pointed spine directed backwards on the sides. Postpetiole broadly convex; petiolar spines arising from the anterior border of the petiole and little curved.

Gaster laterally not marginate, simply with a little protruding anterior border.

Legs. Fore coxae with a tumulus anteriorly. Mid and hind femora without angle or denticles. Mid and hind basitarsi without broad base and not compressed laterally.

Sculpture. Head, mesosoma and pedicel superficially and minutely reticulate-punctate, the reticulation absent on the head dorsum, covered by deep foveae, broader than their interspaces on the two posterior thirds of the head, less impressed on the frontal carinae, on the declivous part of the vertex, on the two anterior thirds of the ventral part of the head, on the pronotum, on the sides of the mesonotum and on the basal face of the propodeum; the same structure sparser on the propleurae, on the middle of the mesonotum and on the basal face of the propodeum; first dorsal third of the head with foveae smaller than those on the two

Fig. 267. *Cephalotes wheeleri* (FOREL). Worker from Cuernavaca, Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

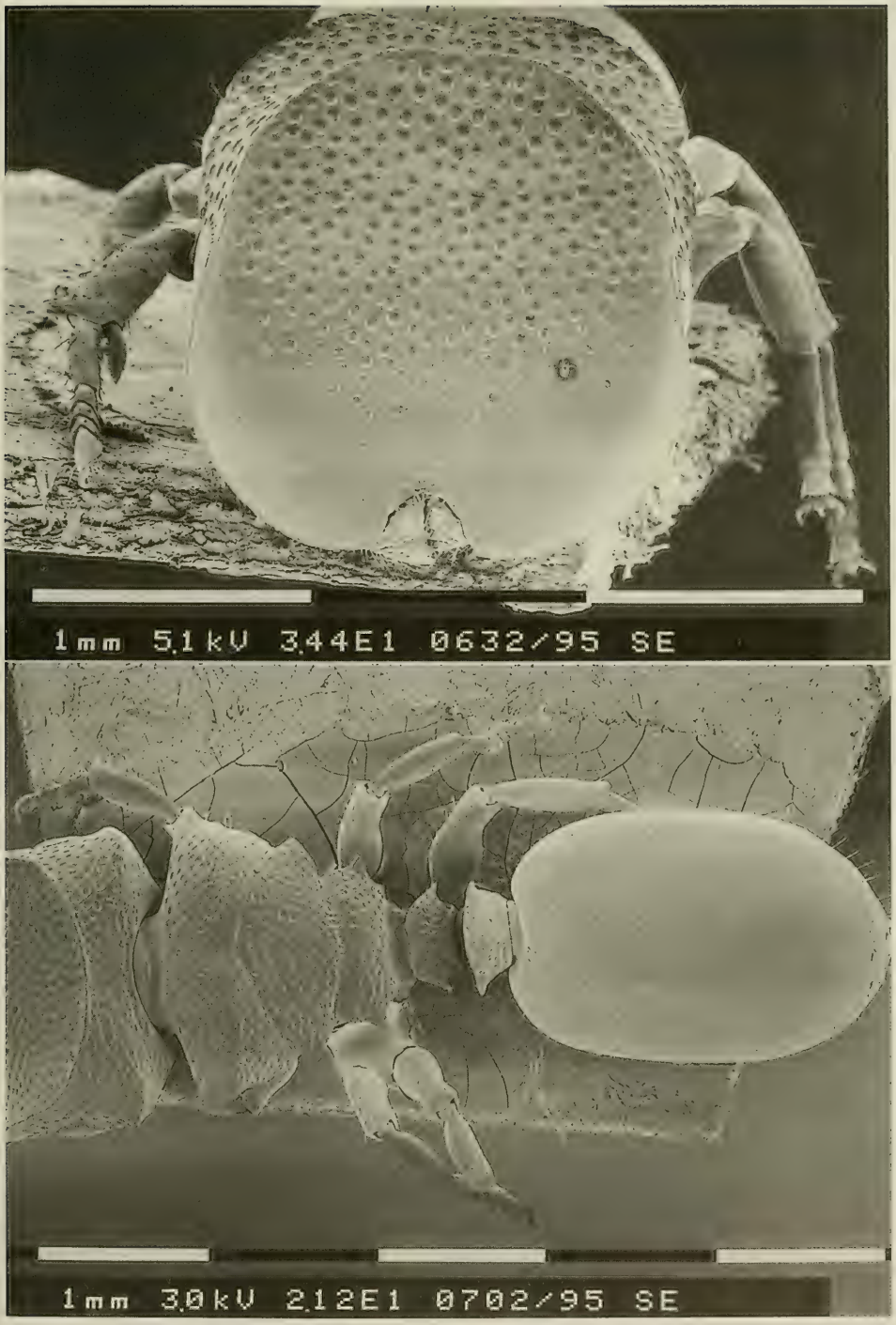


Fig. 268. *Cephalotes wheeleri* (FOREL). Soldier from Cuernavaca, Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

posterior thirds and almost as broad as their interspaces; the foveae oval and shallower on the pedicel. Posterior third of the ventral part of the head, legs, sides of the first gastral tergite, posterior half of the first gastral sternite superficially reticulate-punctate and shining, this sculpture is more impressed on the posterior half of the first tergite and anterior half of the first sternite. Declivous face of the propodeum, meta- and propleurae, anterior half of the first gastral tergite reticulate-punctate and with more or less longitudinal rugulosities. The rugae on the first gastral sternite sometimes are present only on the anterior third of it, or surpassing its first half, and slightly curved to the sides. Outer face of the tibiae with oval and superficial foveae.

Pilosity. Body with three types of hairs: (1) rare, long, erect, truncate on the mesosoma, pedicel and dorsum of the first gastral tergite, sparser on the legs and apex of the gaster, and shorter on the first gastral sternite; (2) decumbent to appressed on each fovea, sparse on the legs, longer and thicker on the pedicel and on the ventral part of the meso- and metapleurae; (3) minute and thin on the gaster.

Colour. Dark brown to black, with reddish-brown frontal carinae, antennae, femora, and lighter tarsi.

Measurements (in mm) and indices: TL 6.04–6.52; HL 1.52–1.56; HW 1.68–1.72; EL 0.36; PW 1.64–1.68; PeW 0.64; PpW 0.68–0.72; HBaL 0.44–0.46; HBaW 0.10–0.11; CI 110.2–110.5; PI 102.4; PPeI 256.2–262.5; PPpI 227.7–247.0; HBaI 22.7–23.9.

M a l e (Previously undescribed). - Head, eyes included, almost 1/3 broader than long; vertexal angles convex. Frontal carinae not raised, strongly diverging backwards and not reaching the first ocellus. Clypeus convex, its anterior border straight. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Mayrian furrows impressed. Propodeum with differentiate basal and declivous faces; basal face convex dorsally and with the sides converging posteriorly; declivous face converging posteriorly and laterally marginate.

Petiole with the anterior face truncate and concave medially; petiole and postpetiole convex dorsally and laterally.

Gaster longer than the mesosoma.

Sculpture. Head and pronotum minutely punctate and with very broad, irregular reticulation. Mesonotum punctate and with superficial foveae surrounded by thin rugosities. Scutellum punctate and with thin, longitudinal rugosities. Basal face of the propodeum and pleurae punctate and with irregular, longitudinal rugosities. Declivous face of the propodeum and gaster superficially reticulate. Pedicel punctate and with thin, longitudinal rugosities slightly irregular on the sides. Legs punctate.

Pilosity. Body with long, pointed hairs, suberect on the head and mesosoma, decumbent on the propodeum, pedicel, gaster and legs.

Colour. The sole available immature specimen is light brown with lighter legs.

Measurements (in mm) and indices: TL 5.58; HL 0.76; HW 0.92; EL 0.39; PW (not measurable: deformed); PeW 0.43; PpW 0.49; HBaL 0.55; HBaW 0.08; CI 121.0; HBaI 14.5.

Note: The description above is based on a single immature and damaged male belonging to the *wheeleri* type series; we did not dare dissecting its genitalia. A few genital characters visible without dissection have been nonetheless included in the data matrix for this species.

M a t e r i a l e x a m i n e d . - **Mexico**: M o r e l o s : Cuernavaca, Dec. 1900, 13 workers (paralectotypes), 8 soldiers [of which lectotype, MZSP, 4 paralectotypes, MCZC, MHNG, MZSP] (lectotype designation by Kempf, 1958a; a soldier in MCZC labelled as lectotype by Kempf in 1950 cannot be considered as such since it does not correspond to the published designation of Kempf, 1958a); same locality, 3 workers (probably syntypes), 2 soldiers (probably syntypes) [MCSN], 1 male [MCZC]; same locality, I.1945, 2 workers, N. L. H. Krauss [USNM].

D i s c u s s i o n . - The closest relative of *C. wheeleri* is *toltecus*. The soldiers of both species can be distinguished from the other soldiers of the *wheeleri* clade by

the floor of the disc flat posteriorly. The soldier of *C. wheeleri*, however, can be distinguished from that of *toltecus* by the absence of a tumulus in the middle of the disc.

Distribution: Mexico.

Cephalotes toltecus DE ANDRADE n. sp.
Figs. 269, 270

Type material: Holotype soldier from 19 mi. NW Magdalena, Jalisco, Mexico, MZSP; paratypes: 3 soldiers and 6 workers, same data as the holotype, all in MZSP.

Derivatio nominis: This species is named after the Toltecs, one of the ancient peoples of south Mexico.

Diagnosis. - A member of the *wheeleri* clade differing from its sister species, *wheeleri*, in the worker by the less regular body rugosities, and in the soldier by the presence of a low, broad tumulus in the middle of the head and by the denser foveae.

Worker (Fig. 269). - Vertexal angles round, with superficially crenulate border. Vertexal border straight and not marginate medially. Hypostoma not connected by a bridge. Cheeks feebly marginate dorsally. Frontal carinae with a superficial incision over the eyes. Antennal scrobes reaching the antero-ventral border of the eyes. Clypeus anteriorly concave. Mandibles with inconspicuous lateral carinae.

Mesosoma gently convex in profile. Pronotum in dorsal view with the anterior border not marginate and convex. Scapular angles absent or not visible in dorsal view. Pronotum with a narrow lamella with three pairs of lateral teeth, the first, humeral, pointed, short and followed by another, smaller, obtuse pair and by a third pair, large, broad and round; the third pair bidentate in some specimens. Sides of the mesonotum converging posteriorly and unarmed. Promesonotal and propodeal sutures superficially impressed only on the sides in dorsal view. Propodeum continuously sloping posteriorly, without distinctly differentiate basal and declivous faces, with a pair of pointed, thin spines directed laterally and slightly upwards at midlength.

Petiole anteriorly truncate; its anterior border marked by a transversal carina variably impressed. Petiolar spines arising from the center of the petiolar sides, shorter than half of the length of the petiole, thin, and pointing backwards. Postpetiole broader than petiole, with thin, pointed spines slightly more than half of the length postpetiole, arising anterolaterally and curved backwards at the base.

Gaster oval, without crest, but superficially marginate on its whole length.

Hind and mid femora without angle or denticles; mid and hind basitarsi long and without flat and broad base.

Sculpture. Head dorsum reticulate, superficially and irregularly foveolate, the foveae denser, deeper and separated by broad reticulation on the posterior third. Frontal carinae much more superficially reticulate than the remaining head dorsum. Ventral face of the head longitudinally striato-rugose. Mesosoma and pedicel reticulate, irregularly foveolate, the foveae separated by broad reticulation anteriorly and with superimposed longitudinal rugosities on the mesonotum and on the propodeum and, on the pedicel among the small specimens. First gastral tergite and sides of the first gastral sternite minutely reticulate and longitudinally rugose, the rugosities more concentric on the middle of the tergite of small specimens; first gastral tergite laterally and center of the first gastral sternite superficially reticulate and shining. Legs reticulate with slightly shining femora. Outer face of the tibiae with oval and superficial foveae.

Pilosity. Body with four types of hairs: (1) sparse, long, erect and truncate, on the head, on the mesosoma, on the pedicel, on the gastral tergites and on the legs; (2) similar to type (1) but thinner and shorter on the gastral sternites; (3) canaliculate, appressed, thick, denser on the vertexal border, on the mesosoma and on the pedicel originating from the foveae; (4) similar to type (3) but shorter and thinner on the frons, on the gaster and on the legs.

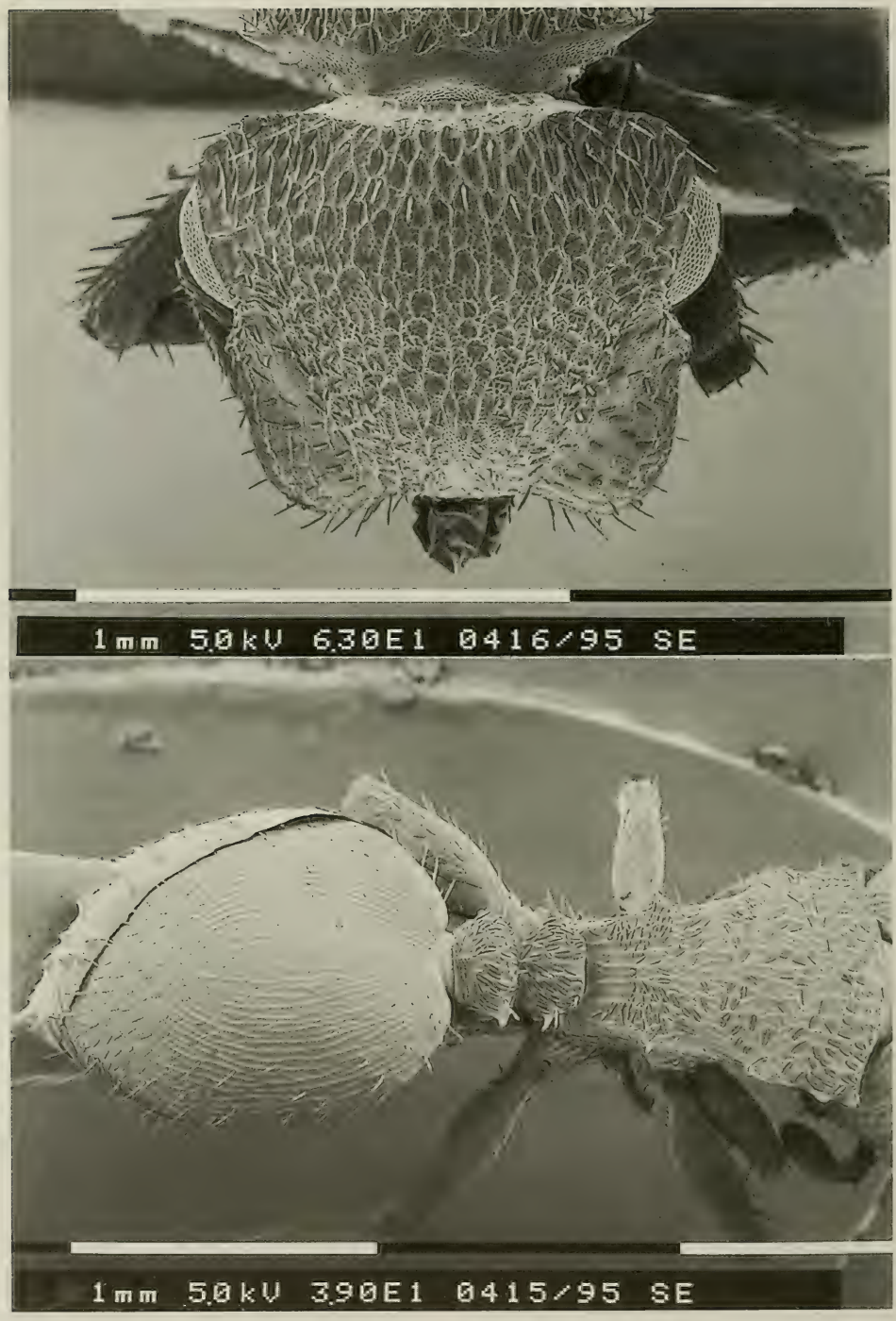


Fig. 269. *Cephalotes toltecus* DE ANDRADE. Worker from Magdalena (Jalisco), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 270. *Cephalotes toltecus* DE ANDRADE. Soldier from Magdalena (Jalisco), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

Colour. Dark brown to black. Frontal carinae yellow and semi-transparent in small and opaque and darker in larger specimens. Antennae, pronotal, propodeal and pedicellar spines and legs reddish-brown. Vertexal angles, propodeum and pedicel with weak golden reflexes due to the pilosity.

Measurements (in mm) and indices: TL 4.16–5.76; HL 0.96–1.28; HW 1.04–1.38; EL 0.28–0.36; PW 0.85–1.28; PeW 0.48–0.68; PpW 0.52–0.80; HBaL 0.40–0.60; HBaW 0.09–0.12; CI 107.8–108.3; PI 107.8–122.3; PPeI 177.1–188.2; PPpI 160.0–163.5; HBaI 20.0–22.5.

S o l d i e r (Fig. 270). - Head disc present. Floor of the disc concave anteriorly, flat posteriorly and with a low tumulus in the middle. Frontal carinae broadly expanded anteriorly, not covering the eyes, converging posteriorly and connected by a sharp, convex, not raised carina on the vertex. Vertexal angles round and marginate. Eyes moderately convex. Clypeal border deeply concave anteriorly. Mandibles laterally carinate and largely hidden by the frontal carinae.

Mesosoma. Humeral angles with a broad, obtuse tooth anteriorly, their sides converging posteriorly. Pronotal carina well marked and superficially interrupted in the middle. Promesonotal suture impressed. Mesonotal sides with a broad, pointed or angulate tooth. Lower mesopleurae without minute denticles. Propodeum with differentiate basal and declivous faces; basal face in dorsal view weakly convex, with a broad, pointed tooth in the middle of each side and narrowing towards the declivous face; declivous face longitudinally concave and bearing a pair of small teeth.

Petiole with distinctly differentiate anterior and posterior faces; anterior face truncate, weakly concave medially; posterior face sloping backwards and bearing laterally a pointed spine directed backwards. Postpetiole broadly convex; postpetiolar spines arising from the anterior border of the postpetiole and slightly curved backwards.

Gaster with a reduced border protruding anteriorly and laterally not marginate.

Legs. Fore coxae with a tumulus anteriorly. Mid and hind femora without angle or denticles. Mid and hind basitarsi without broad base and not compressed laterally.

Sculpture. Head, mesosoma and pedicel superficially and minutely reticulate and foveolate, the foveae deep and broader than their interspaces on the head dorsum, slightly sparser on the anterior half of the pronotum and on the middle of the propodeum, smaller and shallower than on the head dorsum on the posterior half of the pronotum and on the middle of the mesonotum, dense on the sides of the mesosomal dorsum and on the pedicel. Frontal carinae superficially reticulate-foveolate and little shining. Ventral part of the head with the same sculpture as on the anterior part of the pronotum and superficially shining. Pleurae, declivous face of the propodeum, legs, first gastral tergite and sides of the first gastral sternite reticulate; the same sculpture but less impressed than on the legs and more shining on the remaining tergites, sternites and on the middle of the first sternite. Propleurae, lower meso- and metapleurae and outer face of the femora and tibiae with superficial foveae, more irregular on the tibiae. Anterior third of the first gastral tergite and the sides of the first gastral sternite with faint longitudinal rugosities.

Pilosity. Body with four types of hairs: (1) canaliculate, decumbent to appressed arising from each fovea, longer and thicker on the propodeum, on the pedicel and on the lower part of the meso- and metapleurae, slightly shorter and thinner on the extensor face of the legs; (2) long, erect, truncate, rare on the mesosoma and on the pedicel, sparse on the first gastral tergite and on the legs, dense on the posterior border of the gaster; (3) similar to type (2) but shorter and thinner on the first gastral sternite; (4) minute, appressed and thin on the gaster and on the anterior and posterior faces of the legs.

Colour. Black. Frontal carinae dark red. Legs ferruginous with brown first tarsomere and lighter remaining tarsomeres.

Measurements (in mm) and indices: TL 5.96–7.20; HL 1.48–1.64; HW 1.64–1.72; EL 0.34–0.36; PW 1.60–1.68; PeW 0.66–0.68; PpW 0.74–0.76; HBaL 0.46–0.52; HBaW 0.12; CI 104.9–110.8; PI 102.4–102.5; PPeI 242.4–247.0; PPpI 216.2–221.0; HBaI 23.1–26.1.

M a t e r i a l e x a m i n e d . - **Mexico**: Jalisco: 19 mi NW of Magdalena, 3,000', nesting in vine, 01.VIII.1971, 6 workers, 4 soldiers, R. J. HAMTON (type series) [MZSP].

Discussion. - The worker of *C. toltecus* can be distinguished from the other species of the *wheeleri* clade by the reduced but complete margination of the first gastral tergite. Its closest species is *wheeleri* and the soldiers of both species share the posterior part of the disc flat. The soldiers of *C. toltecus* can be distinguished from those of *wheeleri* by the presence of a low tumulus on the disc.

Distribution: Mexico.

Cephalotes insularis (WHEELER) new combination
Figs. 271, 272, 273

Cryptocerus pilosus ssp. *insularis* WHEELER, 1934: 140. Worker. Original description. Type locality: Isla Maria Madre (Tres Marias group, Nayarit, Mexico). Type material: holotype lost, neotype worker from the Maria Magdalena Island (Tres Marias Group) in LACM (SNELLING, 1968). Not seen.

Paracryptocerus insularis (WHEELER), KEMPF, 1958 a: 128. First combination in *Paracryptocerus*.

Paracryptocerus wheeleri (FOREL), KEMPF, 1958 a: 134, pl. 8, figs. 1–2. Soldier. Partim. Nec FOREL. Misidentification detected by SNELLING, 1968: 4.

Cryptocerus insularis WHEELER, SNELLING, 1968: 4, fig. 2. Worker, soldier.

Zacryptocerus insularis (WHEELER), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *wheeleri* clade differing from its sister species, *hirsutus*, by the shorter and sparser appressed hairs of the worker.

Worker (Fig. 271). - Vertexal angles round, with superficially crenulate border. Vertexal border straight and variably marginate medially. Hypostoma not connected by a bridge. Cheeks superficially marginate dorsally. Frontal carinae with a superficial notch over the eyes. Antennal scrobes reaching the antero-ventral border of the eyes. Clypeal border concave. Mandibles with faint lateral carinae.

Mesosoma convex in side view. Pronotum in dorsal view with the anterior border not marginate and convex. Scapular angles absent or not visible in dorsal view. Pronotum with a narrow lamellae bearing three pairs of lateral teeth, the first, humeral, short and pointed, followed by another subequal in length or smaller, variably pointed and by a third broad, obtuse or slightly pointed pair close to the mesonotum. Sides of the mesonotum converging posteriorly and unarmed. Promesonotal and propodeal sutures in dorsal view superficially marked in some specimens only, more impressed on the sides. Propodeum declivous, without distinctly differentiated basal and declivous faces, with a pointed, thin spine directed laterally and slightly upwards at midlength.

Petiole anteriorly truncate; its anterior border marked by a transversal carina variably marked. Petiolar spines ca. half so long as the length of the petiole, thin, pointed backwards and on the middle of the petiolar sides. Postpetiole broader than petiole, with thin, pointed spines slightly shorter than the postpetiolar length, arising anterolaterally and curved backwards at the base.

Gaster oval, without crest, lobe or lateral margin.

Hind and mid femora without angle or denticles; mid and hind basitarsi long and without flat and broad base.

Sculpture. Head dorsum reticulate, with irregular, superficial foveae separated by broad reticulation. Frontal carinae superficially reticulate. Ventral face of the head irregularly striato-rugose and reticulate, the reticulation more impressed in larger specimens. Mesosoma minutely reticulate, irregularly foveolate, the foveae separated by broad reticulation forming longitudinal rugae on the posterior half of the pronotum and on the propodeum; in small specimens the foveae less evident. Same sculpture but more superficial on the pedicel. Sides of the mesosoma with the same sculpture as on the dorsum, but with few or without striae on the upper meso- and metapleurae. First gastral tergite and sides of the first gastral sternite with longitudinal, thin rugosities, irregular and less impressed on the middle of the posterior half

Fig. 271. *Cephalotes insularis* (WHEELER). Worker from the Tres Marias Islands (Nayarit), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

of the first gastral tergite in some specimens. Anterolateral borders of the first gastral tergite and central part of the first sternite superficially reticulate and shining. Legs reticulate, with slightly shining femora. Distal part of the outer face of the femora and outer face of the tibiae with oval and superficial foveae.

Pilosity. Body with four types of hairs: (1) sparse, long, erect and truncate on the head, on the mesosoma, on the pedicel, on the gastral tergites and on the legs; (2) similar to the type (1) but thinner and shorter on the sternites; (3) canaliculate, appressed, thick, denser on the vertexal border, on the mesosoma and on the pedicel; (4) similar hairs to the type (3) but shorter and thinner on the frons, on the gaster and on the legs.

Colour. Dark brown to black. Frontal carinae yellowish to light ferruginous and semi-transparent. Legs orange or ferruginous or light brown with darker basitarsi. Border of the first gastral tergite yellowish and transparent. Some specimens with the anterolateral border of the first gastral tergite with a pair of oval, orange-reddish spots. Vertexal angles, propodeum and pedicel with weak golden reflexes.

Measurements (in mm) and indices: TL 4.08–4.94; HL 1.00–1.20; HW 1.04–1.32; EL 0.28–0.33; PW 0.88–1.18; PeW 0.56–0.62; PpW 0.68–0.74; HBaL 0.44–0.48; HBaW 0.09–0.10; CI 104.0–111.1; PI 111.8–118.2; PPeI 157.1–190.3; PPpI 129.4–159.4; HBaI 20.4–20.8.

S o l d i e r (Fig. 272). - Head disc present. Head dorsum concave, the concavity increasing anteriorly. Middle of the head dorsum with a broad tumulus. Frontal carinae broadly expanded anteriorly, not covering the eyes, strongly converging posteriorly and connected by a sharp, straight ridge on the vertex. Vertexal angles round and marginate. Eyes moderately convex. Clypeal border deeply concave anteriorly. Mandibles laterally carinate and largely hidden by the frontal carinae.

Mesosoma. Humeral angles with a broad, angulate tooth anteriorly, their sides converging posteriorly. Pronotal carina marked and interrupted in the middle. Promesonotal suture impressed. Mesonotal sides with a broad tooth with round or pointed tip. Lower mesopleurae without denticles. Propodeum differentiated in basal and declivous faces; basal face in dorsal view poorly convex, with a broad, pointed tooth in the middle of each side and narrowing towards the declivous face; declivous face longitudinally concave.

Petiole with distinctly differentiated anterior and posterior faces; anterior face truncate, posterior face slightly convex and bearing, on its sides, a pointed spine directed backwards. Postpetiole broadly convex; postpetiolar spines broad, pointed, arising from the anterior border of the postpetiole and slightly curved backwards.

Gaster with a barely protruding anterior border and laterally not marginate.

Legs. Fore coxae with a tumulus anteriorly. Mid and hind femora without angle or denticles. Mid and hind basitarsi without broad base and not compressed laterally.

Sculpture. Head and mesosoma reticulate-punctate, with superimposed foveae broader than their interspaces, diminishing in size on the anterior part of the head and more superficial on the frontal carinae. Pedicel reticulate and with dense foveae, in some specimens this sculpture extends to the sides of the mesosoma. Pleurae reticulate, superficially foveolate and with few rugosities, the foveae rare on the metapleurae. Two posterior thirds of the declivous face of the propodeum, gaster and legs reticulate, the reticulation fainter on the femora and on the posterior half of the first gastral sternite. Anterior third of the first gastral tergite with longitudinal rugosities; most specimens bear similar rugosities but more superficial on the sides or on the anterior third of the first gastral sternite. Outer face of the tibiae with oval and superficial foveae.

Pilosity. Body with four types of hairs: (1) decumbent to appressed arising from each fovea, longer and thicker on the propodeum, on the pedicel and on the lower part of the meso- and metapleurae, slightly shorter and thinner on the extensor face of the legs; (2) long, erect, truncate, rare on the pedicel, sparse on the first gastral tergite and on the legs, dense on the posterior border of the gaster; (3) similar to type (2) but shorter and thinner on the first gas-tral sternite; (4) minute, appressed and thin on the gaster and on the anterior and posterior faces of the legs.

Colour. Black. Frontal carinae dark red. Some specimens with the dorsal side of the head dark red. Legs ferruginous with brown tarsi. Some specimens with the antero-lateral border

Fig. 272. *Cephalotes insularis* (WHEELER). Soldier from the Tres Marias Islands (Nayarit), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

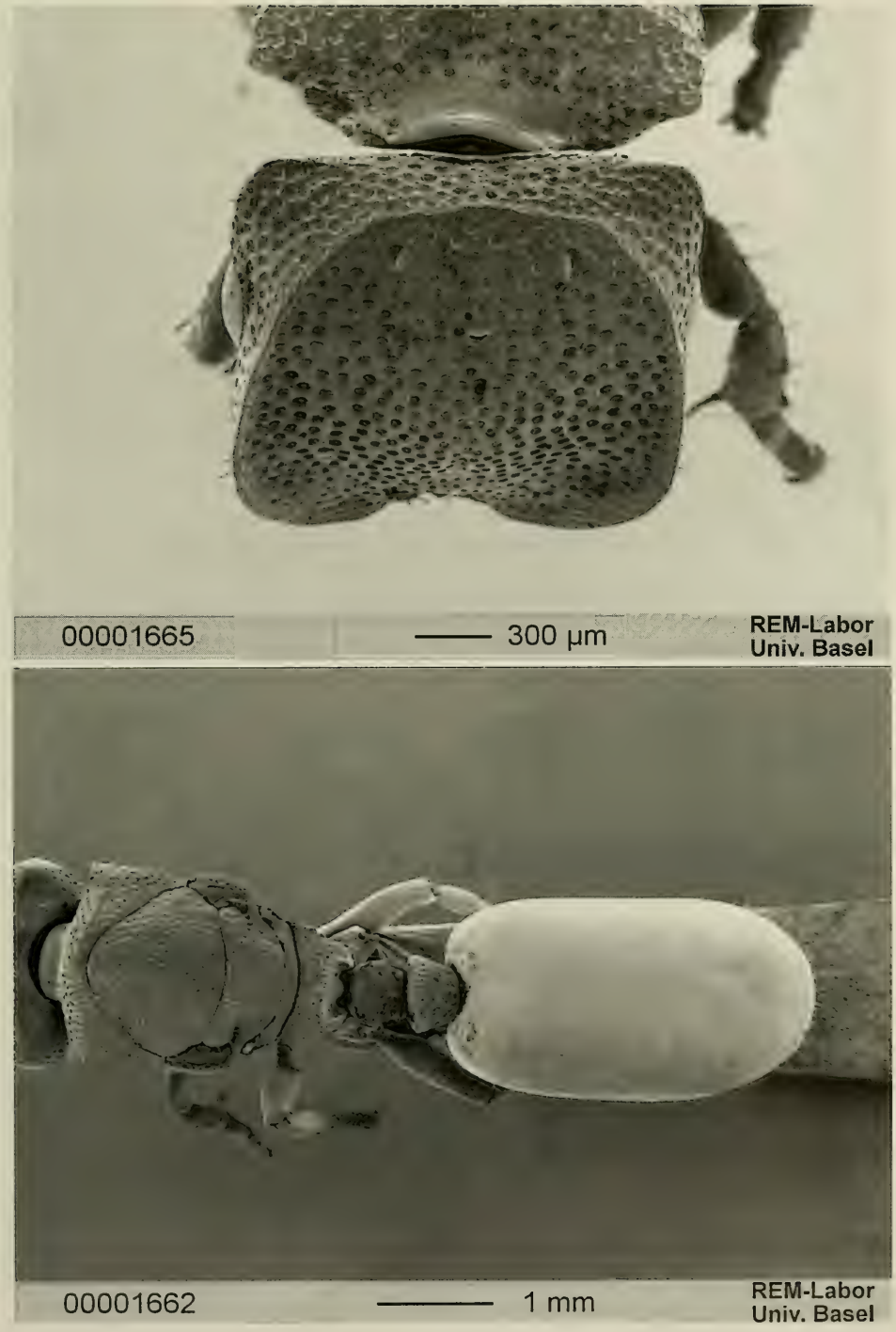


Fig. 273. *Cephalotes insularis* (WHEELER). Gyne from Mexico (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

of the first gastral tergite with a pair of oval, reddish spots or with the border of the first gastral tergite yellowish and transparent.

Measurements (in mm) and indices: TL 6.60–6.84; HL 1.64–1.68; HW 1.76–1.84; EL 0.36–0.37; PW 1.80; PeW 0.71–0.74; PpW 0.80–0.88; HBaL 0.46–0.48; HBaW 0.13; CI 107.3–109.5; PI 97.7–102.2; PPeI 243.2–253.5; PPpI 204.5–225.0; HBaI 27.1–28.3.

G y n e (Fig. 273) (previously undescribed). - Head disc present. Posterior two thirds of the head dorsum gently convex. Anterior third of the head concave. Frontal carinae anteriorly broadly expanded and with raised border, converging posteriorly and connected by a convex carina on the vertex. Vertexal angles round and marginate. Eyes convex and not hidden by the disc in dorsal view. Anterior clypeal border concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma flat in side view. Humeral angles with an obtuse tooth anteriorly, straight posteriorly. Pronotal carina marked and superficially interrupted in the middle. Promesonotal suture impressed. Propodeum differentiated in basal and declivous face; basal face weakly convex dorsally, with the sides bearing a small denticle medially; sides of the declivous face converging posteriorly.

Petiole distinctly differentiated in anterior and posterior faces; anterior face truncate, posterior face slightly convex and with the sides bearing a minute denticle medially. Postpetiole broadly convex; postpetiolar spines broad, obtuse and arising from the anterior border of the postpetiole

Legs and gaster. As in the soldier.

Sculpture. Head, pronotum, mesonotum and scutellum reticulate-punctate and with foveae broader than their interspaces, slightly sparse on the middle of the mesopleurae and on the anterior half of the ventral part of the head Propodeum, upper mesopleurae and pedicel reticulate and with dense foveae. Propleurae and metapleurae reticulate and with sparse foveae on the propleurae and rare on the metapleurae. Two posterior thirds of the declivous face of the propodeum, gaster and legs reticulate, the reticulation fainter on the femora and on the posterior half of the first gastral sternite. Anterior third of the first gastral tergite with longitudinal rugosities; similar rugosities but more superficial on the sides of the anterior third of the first gastral sternite. Outer face of the tibiae with oval and superficial foveae.

Pilosity. As in the soldier except for the presence hair type (2) on the border of the frontal carinae and of the vertexal angles and on the mesosoma.

Colour. Head reddish, gaster darker. Mesosoma and pedicel dark brown. Legs ferruginous with brown tarsi.

Measurements (in mm) and indices: TL 8.24; HL 1.68; HW 1.76; EL 0.39; PW 1.70; PeW 0.58; PpW 0.67; HBaL 0.53; HBaW 0.15; CI 104.8; PI 103.5; PPeI 293.1; PPpI 253.7; HBaI 25.9.

M a t e r i a l e x a m i n e d . - **Mexico**: no further locality, intercepted in Nogales, Arizona, 02.II.1968, 8 workers, 3 soldiers, 1 gyne, in legumes (stem), J. M. KAISER [USNM]; N a y a r i t : Maria Magdalena Island (Tres Marias group), 26.III.1964, 5 workers, 1 soldier, R. R. SNELLING [MZSP].

D i s c u s s i o n . - *C. insularis* is the sister species of *hirsutus*. Both share the postpetiolar spines almost as long as the postpetiole and the border of the first gastral tergite yellowish and transparent. Some of the workers intercepted in Nogales present a pair of distinct brownish spots on the anterior face of the gaster; other specimens from the same series don't. The gastral spots, according to our phylogenetic reconstruction, should have been secondarily lost among the members of the *wheeleri* clade.

D i s t r i b u t i o n : Mexico.

Cephalotes hirsutus DE ANDRADE n. sp.
Fig. 274

Type material: Holotype worker from 4.6 mi E of Chupaderos, Sinaloa, Mexico, 22.8.1964, E. I. SCHLINGER; paratypes 3 workers, same data as the holotype, all in LACM.

Derivatio nominis: *hirsutus* in Latin means hairy, referred to the abundant pilosity of this species.

Diagnosis. - A member of the *wheeleri* clade the worker of which differs from all the other species of the clade for possessing the following autapomorphy: body with dense, thick, long, appressed hairs with golden reflexes.

Worker (Fig. 274). - Vertexal angles round, with superficially crenulate border. Vertexal border straight and not marginate medially. Hypostoma not connected by a bridge. Cheeks feebly marginate dorsally. Frontal carinae with a superficial incision over the eyes. Antennal scrobes reaching the antero-ventral border of the eyes. Clypeal border concave. Mandibles with superficial lateral carinae.

Mesosoma convex in profile. Pronotum in dorsal view with the anterior border not marginate and convex. Scapular angles absent or not visible in dorsal view. Pronotum with three pairs of lateral teeth, the first, humeral, short and pointed, followed by another pair subequal in length or smaller, variably pointed and by a third, shorter, broad, obtuse or round pair close to the mesonotum. Sides of the mesonotum converging posteriorly and unarmed. Promesonotal and propodeal sutures superficially marked only on the sides in dorsal view. Propodeum continuously sloping posteriorly, without distinctly differentiated basal and declivous faces, with a pair of pointed, thin spines directed laterally and slightly upwards at midlength.

Petiole anteriorly truncate; its anterior border marked by a transversal carina variably impressed. Petiolar spines on the middle of the petiolar sides, ca. half as long as the petiole, thin, and pointing backwards. Postpetiole broader than petiole, with thin, pointed spines slightly shorter than the postpetiole, arising anterolaterally and curved backwards at the base.

Gaster oval, without crest, lobe or lateral margin.

Hind and mid femora without angle or denticles; mid and hind basitarsi long and without flat and broad base.

Sculpture. Head dorsum reticulate, with dense, irregular foveae divided by thick, reticulation, sometimes forming longitudinal, irregular rugosities. Frontal carinae superficially reticulate. Ventral face of the head reticulate and irregularly striato-rugose. Mesosoma and pedicel reticulate, with foveae separated by irregular, longitudinal striae and rugae. Sides of the mesosoma with the same sculpture as the dorsum, but with rare foveae. Upper metapleurae with or without striae on the. First gastral tergite and sides of the first gastral sternite with longitudinal, thin rugosities, more superficial and irregular posteriorly in some specimens Anterolateral borders of the first gastral tergite and central part of the first sternite superficially reticulate and shining. Legs reticulate, with slightly shining femora. Outer face of the tibiae with oval and superficial foveae.

Pilosity. Body with four types of hairs: (1) sparse, long, erect and truncate on the head, on the mesosoma, on the pedicel, on the gastral tergites and on the legs; (2) similar to type (1) but thinner and shorter on the gastral sternites; (3) canaliculate, long, appressed, thick and dense, on the head, on the dorsum of the mesosoma, on the pedicel, on the first gastral tergite and on the extensor face of the legs; (4) similar to the type (3) but thinner and shorter on the middle of the first gastral tergite, on the first gastral sternite and on the anterior and posterior faces of the legs.

Colour. Black. Frontal carinae yellowish orange and semi-transparent. Fore legs with tibiae and tarsi ferruginous. Femora and tarsi of the mid and hind legs black. Tibiae and tarsomeres of the mid and hind legs dark ferruginous with the tarsomeres lighter. Border of the first gastral tergite yellowish and transparent. Some specimens with the antero lateral

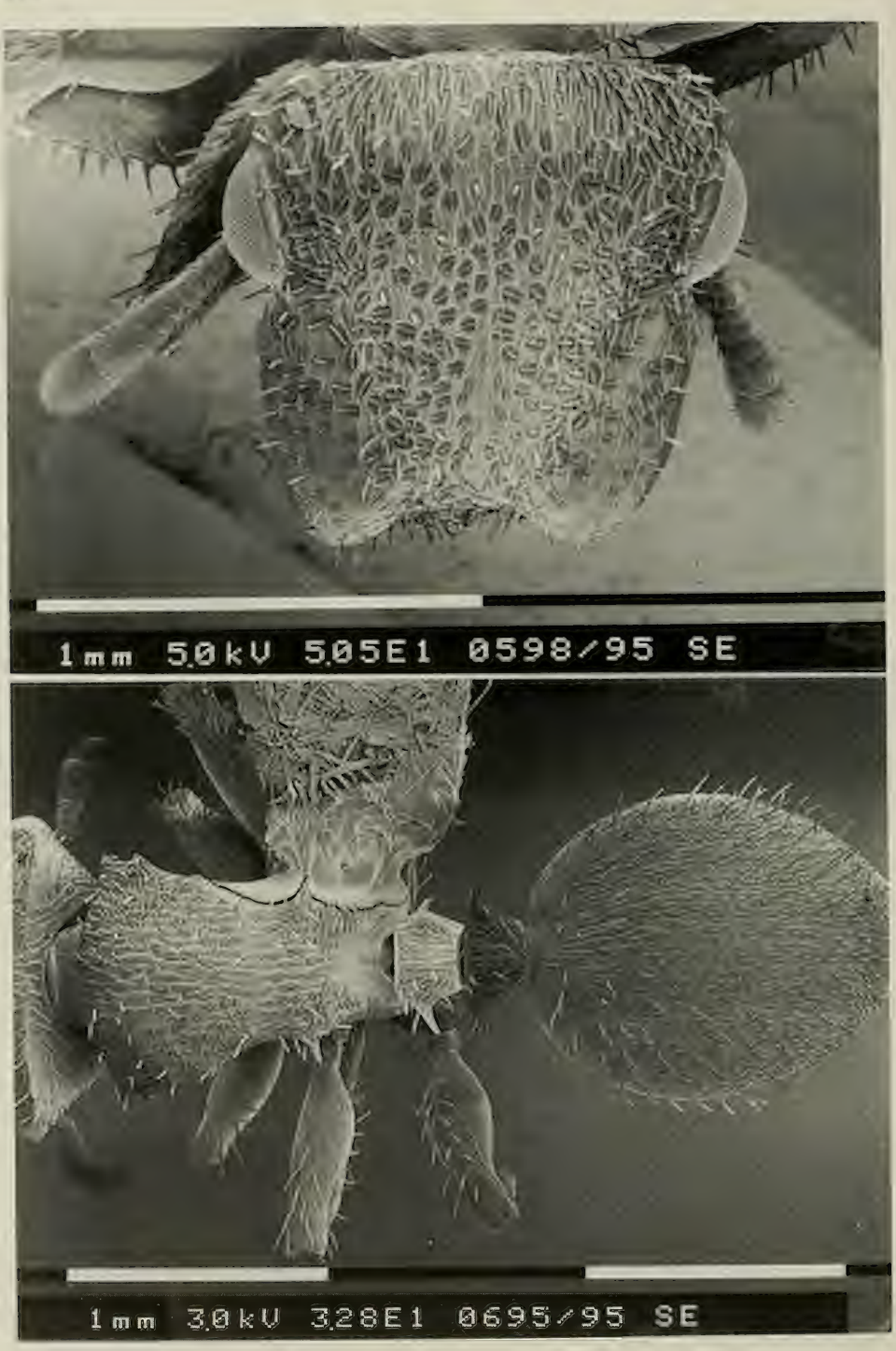


Fig. 274. *Cephalotes hirsutus* DE ANDRADE. Worker from Chupaderos (Sinaloa), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

border of the first gastric tergite with a pair of oval, orange-reddish spots. Golden reflexes due to the pilosity on most of the body including the appendages.

Measurements (in mm) and indices: TL 4.58–4.92; HL 1.08–1.14; HW 1.18–1.26; EL 0.32–0.34; PW 0.96–1.08; PeW 0.53–0.57; PpW 0.68–0.68; HBaL 0.52; HBaW 0.11; CI 109.0–110.5 PI 116.7–122.9; PPeI 181.1–189.5; PPpI 143.3–158.8; HBaI 21.1.

Material examined. - **Mexico**: Sinaloa: 4.6 mi E Chupaderos, 22.8.1964, 4 workers (holotype and paratypes), E. I. SCHLINGER [LACM].

Discussion. - *C. hirsutus* is the sister species of *insularis*. Both share the postpetiolar spines subequal in length to the postpetiole and the border of the first gastral tergite yellowish and transparent. *C. hirsutus* can be easily differentiated from all other species of the *wheeleri* clade for having the body with dense, thick, long, appressed hairs with golden reflexes. Additional characters distinguishing *hirsutus* from its sister species, *insularis*, are given under *insularis*.

Distribution: Mexico.

5.6.20. The *texanus* clade

A small clade (6 species) comparable under several respects to its sister clade, *wheeleri*. Its members, however, lack the six synapomorphies characteristic of the *wheeleri* clade and are grouped together by the following ones, absent in the latter: worker propodeum with three pairs of lateral denticles and, presumably, in spite of the limited evidence available, the internal border of the aedeagus narrowly concave. There is abundant presumptive evidence suggesting that most species of this clade should be obligatory inhabitants of epiphytes. These species range from southern United States up to Costa Rica to the south.

Species included in the clade: *auriger*, *chacmul*, *curvistriatus*, *lenca*, *sobrius*, *texanus*.

Cephalotes texanus (SANTSCHI) new combination
Figs. 384 A, 385

Cryptocerus texanus SANTSCHI, 1915: 208, fig. 2. Worker and soldier. Original description. Type locality: Texas. Type material: one worker and two soldiers from Texas, without further locality, J. BONDROIT (NHMB), examined.

Cryptocerus texanus SANTSCHI, SMITH, 1947 a: 30. Worker and soldier, gyne, male.

Cryptocerus texanus SANTSCHI, CREIGHTON & GREGG, 1954: 47, figs. 1–3, pls. 3–4. Worker, soldier, gyne.

Paracryptocerus texanus (SANTSCHI), M. R. SMITH, 1951: 825. First combination in *Paracryptocerus*.

Paracryptocerus texanus (SANTSCHI), KEMPF, 1958 a: 123, pl. 2, fig. 5, pl. 4, fig. 4, pl. 6, fig. 7. Worker and soldier.

Paracryptocerus texanus (SANTSCHI), KRAFCHICK, 1959: 63, fig. 20 (penis valve), 69, fig. 4 (male paramere).

Zacryptocerus texanus (SANTSCHI), BUREN et al., 1977: 101, fig. 1. Soldier. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *texanus* clade characterised, in the worker, by the irregular rugosities on the ventral part of the head and by the anterior face of the petiole without denticles, and, in the soldier and gyne, by the contiguous foveae on the disc.

Worker (description of SMITH, 1947 a). - "Length 3.6–4 mm.

Posterior border of head weakly emarginate, posterolateral corners not excised, dorsal surface largely convex except toward the sides, anterior border with a distinct emargination exposing much of the mandibles. Promesonotal suture lacking or very poorly indicated, mesoepinotal suture present but not strongly developed. Thorax marginate on each side, bearing spines arranged in the following order: Two on pronotum, one on mesonotum, and two on epinotum (the anterior one lying near the mesoepinotal suture and sometimes feebly developed). Petiolar and postpetiolar nodes and also their spines similar to those of the soldier but smaller, the postpetiolar spines usually less reflexed apically. Gaster as in soldier.

Pitlike impressions on head and thorax smaller and more irregular than in soldier, the sculpturing on the thorax especially with a reticulate-rugose trend. Sculpture on gaster similar to soldier's.

Pilosity similar to that of the soldier in nature and arrangement.

Black; mandibles, frontal carinae, antennae, apex of each femur, tibiae, and all tarsal segments except the basitarsal reddish brown. Frontal carinae and a basal spot on each side of gaster whitish yellow. The spot on each side near the posterior border of the first gastral segment, which is sometimes present in the soldier, apparently missing in the worker."

Measurements (in mm) and indices: TL 3.20–4.64; HL 0.82–1.12; HW 0.88–1.20; EL 0.24–0.30; PW 0.79–1.12; PeW 0.36–0.52; PpW 0.45–0.64; HBaL 0.32–0.40; HBaW 0.07–0.09; CI 107.1–108.0; PI 107.1–112.5; PPeI 192.0–219.4; PPpI 165.5–175.5; HBaI 21.9–24.3.

S o l d i e r (Fig. 384 A, 385) (description of SMITH, 1947 a). - "Length 4.5–5.4 mm.

Cephalic disc proportionately broader than in *rohweri*, approximately as broad as long, with posterior border usually weakly emarginate, occasionally straight, posterolateral corners oblique, sides less subparallel and front rounded, bearing a distinct median emargination which exposes much of the mandibles. A convexity near the center of the disc. Border weakly or not crenulate. Pronotum as broad as head. Transverse pronotal crest well developed, sharp but interrupted in the middle, somewhat crenate; lateral border of pronotum usually spineless, except for a very feeble indication of an anterolateral spine. Promesonotal and mesoepinotal sutures weakly to moderately well indicated, the mesoepinotal suture usually the more distinct of the two. Mesonotum projecting laterally as a short, angular lobe. Epinotum concave posteriorly, each lateral margin with three lobes, if one includes the anterolateral and posterolateral corners, the median lobe larger than the other two. Each side of petiolar and postpetiolar nodes with a short spine, that on the postpetiolar node usually larger and more strongly reflexed posteriorly. Gaster oblong, with a very distinct basal emargination, and with weakly developed anterolateral margins.

Pitlike impressions on the head and thorax much smaller, finer and apparently less circular than in *rohweri*. Gaster very finely granulate, but lacking the rugulae of *rohweri*.

Gaster beneath and apically with short, erect hairs; rest of body and appendages apparently devoid of hair except a few on the pronotal crest. Body and appendages with short, appressed, silvery hairs, the pitlike impressions on head and thorax each bearing only one of these hairs.

Black; mandibles, antennae, frontal carinae, occasionally the entire border of the cephalic disc, apex of each femur, tibiae, tarsi, and sometimes a spot on each side near to the posterior border of the first gastral segment reddish brown, in addition there is always a whitish-yellow basal spot on each side of the gaster."

Measurements (in mm) and indices: TL 5.20–5.72; HL 1.28–1.40; HW 1.42–1.56; EL 0.30–0.32; PW 1.46–1.56; PeW 0.56–0.60; PpW 0.68–0.72; HBaL 0.37–0.39; HBaW 0.10–0.11; CI 110.9–111.4; PI 97.3–100.0; PPeI 260.0–260.7; PPpI 214.7–216.7; HBaI 27.0–28.2.

G y n e (description of SMITH, 1947 a). - "Length 6–6.6 mm.

Smaller than *rohweri*. Impressions on head and thorax smaller, finer and less circular. Mandibles, frontal carinae, antennae, tibiae, and all of tarsal segments except the basitarsal, reddish brown; basal spot on each side of gaster whitish yellow (body of *rohweri* entirely black). Silvery, appressed hairs conspicuous over the body and appendages, these lacking in *rohweri*. Anterolateral corners of pronotum not so acute. Epinotum concave posteriorly (straight in

rohweri). Postpetiolar node more compressed anteroposteriorly and with much larger and more prominent spines. Differing from soldier and worker (of *texanus*) in having sparse, short, suberect to erect hairs on thorax, postpetiole, and gaster.

Description based on a wingless female."

Measurements (in mm) and indices: TL 6.24–7.20; HL 1.32–1.50; HW 1.28–1.52; EL 0.32–0.36; PW 1.28–1.48; PeW 0.55–0.68; PpW 0.70–0.85; HBaL 0.43–0.48; HBaW 0.11–0.13; CI 97.0–101.3; PI 100.0–102.7; PPeI 217.6–232.7; PPpI 174.1–182.8; HBaI 25.6–27.1.

Male (description of SMITH, 1947 a). - "Length 4–4.7 mm.

Eye convex, longer than broad. Posterior border of head rounded, with the ocelli borne on summit. Antenna 13-segmented, the segments enlarging toward the apex but not forming a definite club; scape short, first funicular segment annular. Mesonotum with well-developed Mayrian furrows. Epinotum with coarse longitudinal rugulae. Venation similar to that of *rohweri* female. Side of petiolar and postpetiolar node each with a small tubercle; the tubercles not very noticeable under the low power of binocular. Gaster from above, subelliptical, broadest at base. Pronotum and mesonotum especially, with coarse impressions in addition to other sculpturing.

Body subopaque. Sides of thorax, petiole, postpetiole, coxae, trochanters, femora, and gaster shining.

Head, thorax, petiole, and postpetiole with rather long, greyish, erect, simple hairs; hairs on legs less abundant and more appressed.

Body black. Antenna yellow except for a slight infuscation on scape and first funicular segment. Wings hyaline, legs and genital appendages lighter than body."

Material examined. - **United States**: Texas: unknown locality: 1 worker (syntype), 2 soldiers (syntypes), BONDROIT [NHMB]; George West, 4 mi S and W Live Oak Co., 12.I.1968, 5 workers, 8 soldiers, 2 gynes, R. R. SNELLING [MHNG, MZSP]; George West, 19.XI.1964, in *Quercus virginiana*, 4 workers, 4 soldiers, 4 gynes, W. S. CREIGHTON [MCZC]; Lapara Creek, Live Oak Co., 28.11.1951, in *Quercus virginiana,* 1 worker, 1 soldier, 1 gyne, W. S. CREIGHTON [MZSP]; Gambel Creek, Live Oak Co., 28.XI.1951, in *Quercus virginiana,* 2 workers, 1 soldier, W. S. CREIGHTON [MZSP]; Columbus, 14.VII.1942, 10.VIII.1942, 14 workers, 11 soldiers, 1 gyne, Wm. F. BUREN [MZSP]; Victoria Co., 1 worker, 1 soldier, MITCHELL [MZSP]; Floresville, 14.12.1951, *Quercus virginiana*, 2 workers, 1 soldier, W. S. CREIGHTON [MZSP]; 4 mi W of Sealy, 03.XII.1951, in *Quercus virginiana,* 1 worker, 2 soldiers, W. S. CREIGHTON [MZSP]; Hochheim, De Witt Co., 13.XII.1951, in *Quercus stellata,* 2 workers, 1 soldier, W. S. CREIGHTON [MZSP]; Weslaco, Jul.-Aug. 1946, 3 workers, 3 soldiers, R. ROBERTS [MCZC]; Browsville, 11–16.VI.1933, 5 workers, DARLINGTON [MCZC].

Mexico: Nuevo León: Montemorelos, El Pastor, 2200', 12.2.1952, in *Quercus fusiformis*, 2 workers, 1 soldier, W. S. CREIGHTON [MZSP]; Linares, 2300', 12.II.1952, in *Quercus fusiformis*, 2 workers, 1 soldier, W. S. CREIGHTON [MZSP].

Discussion. - This is the most frequently collected species of the clade. It appears in outgroup position as compared with the other species of the clade and, in general habitus, it is the species resembling more the species of the sister clade *wheeleri*.

Distribution: Texas, North Mexico.

Cephalotes curvistriatus (FOREL) new combination

Figs. 275, 276, 277, 278, 279, 280

Cryptocerus curvistriatus FOREL, 1899 a: 52. Worker. Original description. Type locality: Turrialba, Costa Rica. Type material presumably lost; not found neither in MHNG nor in MCSN.

Paracryptocerus curvistriatus (FOREL), KEMPF, 1958 a: 114, pl. 2, fig. 7, pl. 4, fig. 3, pl. 5, fig. 5, pl. 6, figs. 2, 11, 14. Worker and soldier, gyne. First combination in *Paracryptocerus*.

Zacryptocerus curvistriatus (FOREL), HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *texanus* clade differing from its nearest outgroup species, *texanus*, in the worker by the thick, regular striae on the ventral part of the head, and from the closest ingroup species, *lenca* and *sobrius*, by the hind femora not angulate. The soldier differs from *texanus* by the foveae on the disc sparser and from that of *sobrius* for the foveae on the disc denser.

W o r k e r (Fig. 275) (description of KEMPF, 1958 a). - "Total length 4.2–4.8 mm; maximum length of head 1.18–1.36 mm; maximum length of thorax 1.21–1.43 mm. Black; the following ferruginous: tip of mandibles, tip of scape, basal funicular segment, tip of apical funicular segment, tarsites II - V; testaceous: frontal carinae, tip of femora, extensor face of tibiae, maculae of gaster, tip of thoracic teeth and peduncular spines.

Head opaque, subquadrate, maximum length of head subequal to, often slightly exceeding, the interocular width. Clypeal sutures vestigial. Lateral border of head sinuous in front of, upturned above eyes. Occipital lobes broadly obliquely truncate. Occipital border emarginate. Head gently convex above. Dorsum of head finely reticulate-punctate, rather densely foveolate, or even reticulate foveolate. Lower face of head regularly and coarsely longitudinally striate.

Thorax opaque. Anterior border arched in the middle, concave at the sides. Scapular angle incorporated in the lateral, tridentate border of pronotum. The two anteriormost teeth closer together, triangular, acute, somewhat foliaceous, the posterior tooth on the posterior corner either subrectangular or pointed, in the latter case pointing obliquely caudad. Promesonotal suture vestigial or obsolete, indicated at most by the lack of scalelike hair. Mesonotum with a very small denticle on each side, practically unarmed. Mesoepinotal suture as promesonotal suture, absent or marked merely by a lack of scalelike hair. Lateral border of basal face tridentate, the anterior two teeth very distinct, the second largest, the third tooth, on the junction of the declivous face, minute. Dorsum of thorax coarsely and longitudinally striato-rugose, reticulate-rugose in front, near the anterior border of pronotum. Declivous face neither excavate, nor distinctly marginate on its borders, but longitudinally striate. Pleura horizontally striato-rugose. Outer face of fore femora longitudinally or obliquely striato-rugose.

Peduncular segments opaque, sculptured as dorsum of thorax, except for he lower face which is longitudinally striate. Petiole with a vertically truncate, finely reticulate-punctate, anterior face, which terminates above on each side with a projecting small denticle. Lateral processes spinelike, their apices gently curved, and acute. Postpetiole broader than petiole, its dorsum gently convex, its lateral spines very long, their apices more, but never strongly, recurved.

Gaster opaque, oval, emarginate anteromesially. The broad, scarcely prominent anterolateral lobes with a hyaline, narrow crest on their border, which extends backwards to the level of the stigma.

Lateral border of gaster bluntly marginate beyond the anterior half of first tergite. Dorsum of gaster finely reticulate, with larger, mostly longitudinal, yet occasionally anastomosing rugosities, much finer than on thorax. First sternite smooth and shiny distally, longitudinally striate laterad, the striae converging behind in front of the posterior border forming concentric arches.

Standing hair on tip of gaster, anterolaterally and above the eyes on the lateral border of head. Scalelike hair canaliculate, silvery, appressed, highly shiny, in foveolae of head, between the costae of thorax, and on dorsum of peduncle and gaster, and on extensor face of femora and tibiae. Usually simple, always smaller on sides of legs, on lower face of head, and on first gastral sternite."

Measurements (in mm) and indices: TL 4.28–5.04; HL 1.04–1.20; HW 1.16–1.36; EL 0.28–0.30; PW 1.04–1.20; PeW 0.58–0.64; PpW 0.74–0.69; HBaL 0.40–0.51; HBaW 0.09–0.12; CI 110.0–113.3; PI 111.5–117.8; PPeI 179.3–187.5; PPpI 150.7–157.9; HBaI 22.5–25.0.

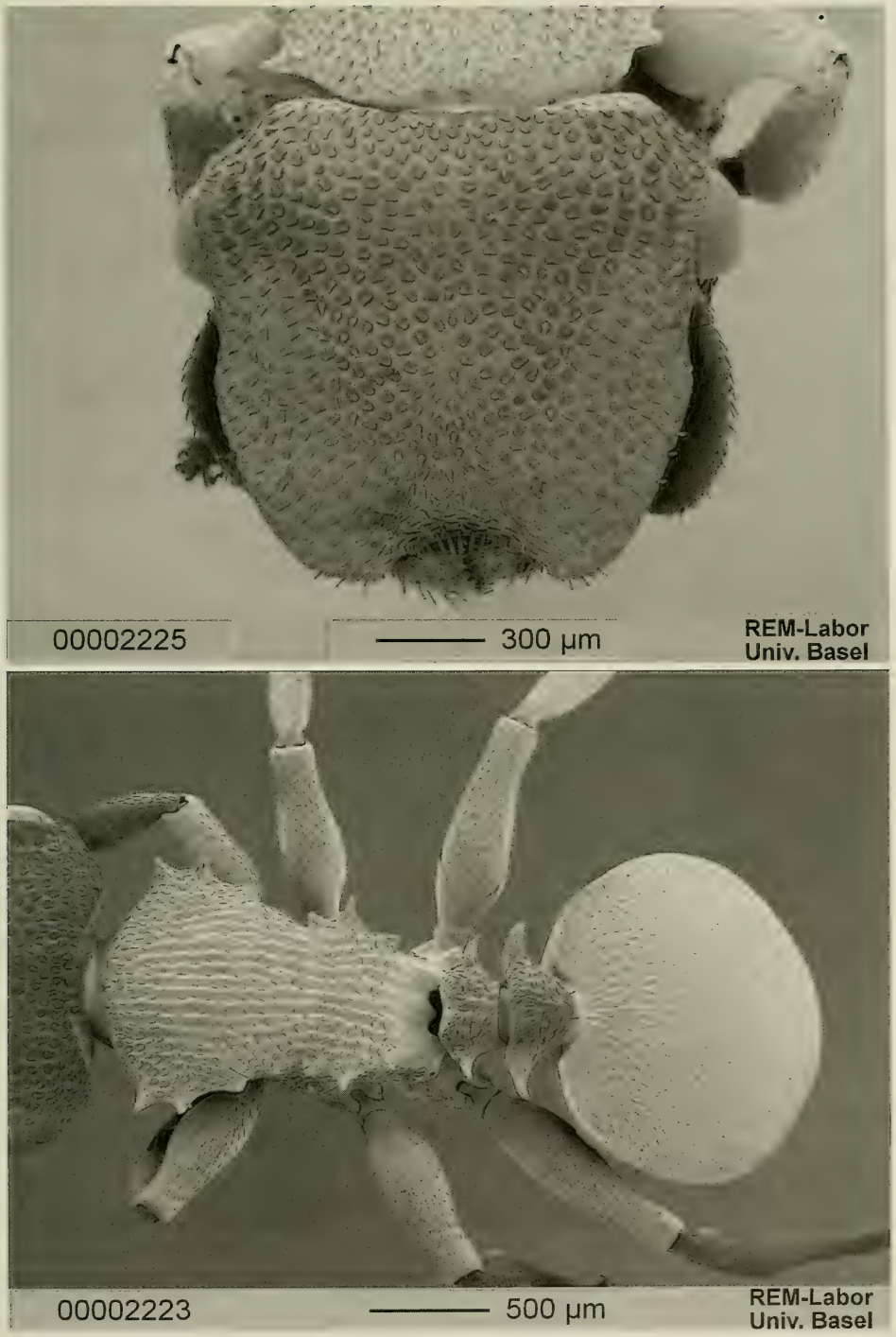


Fig. 275. *Cephalotes curvistriatus* (FOREL). Worker from Costa Rica (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

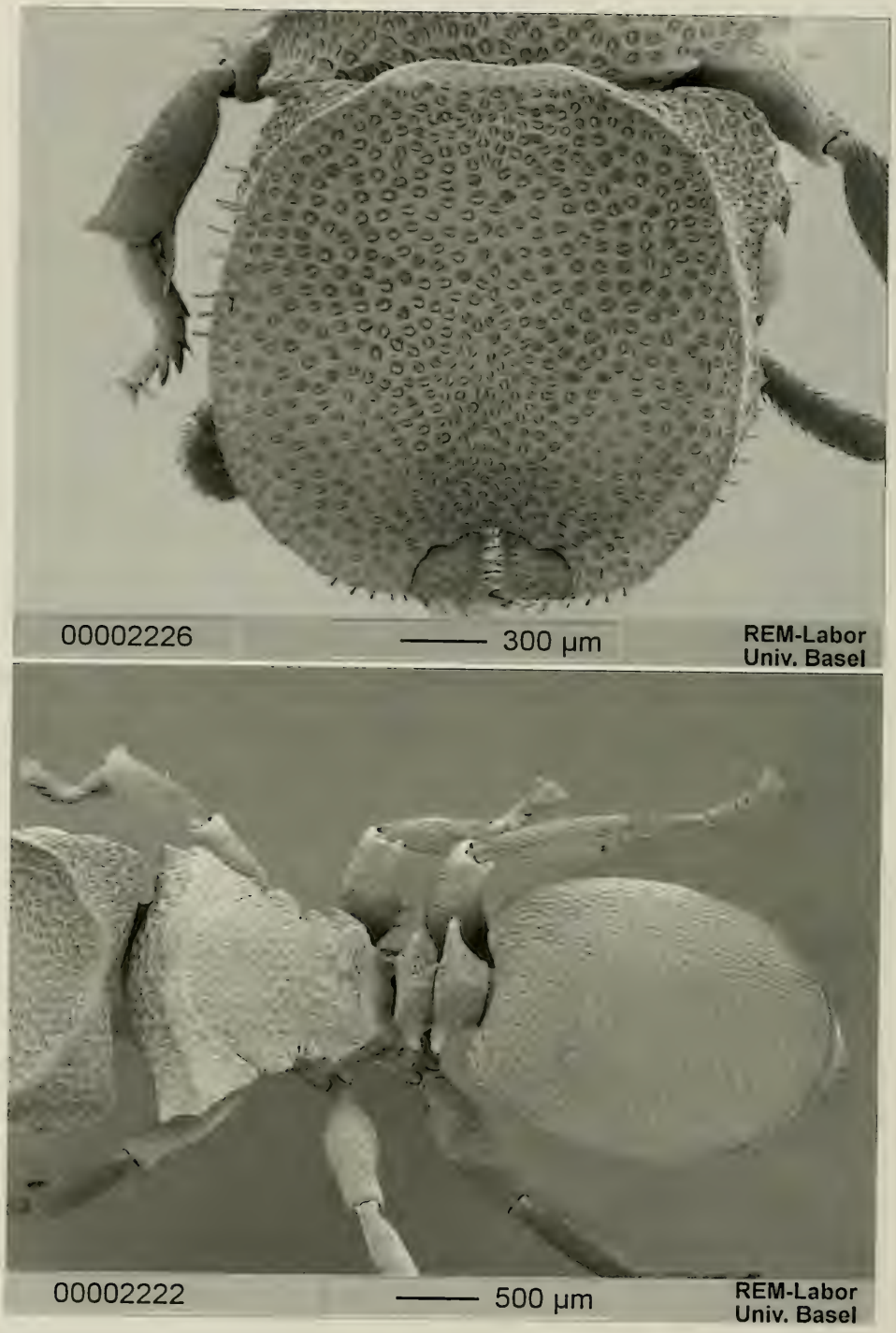


Fig. 276. *Cephalotes curvistriatus* (Forel). Soldier from Costa Rica (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

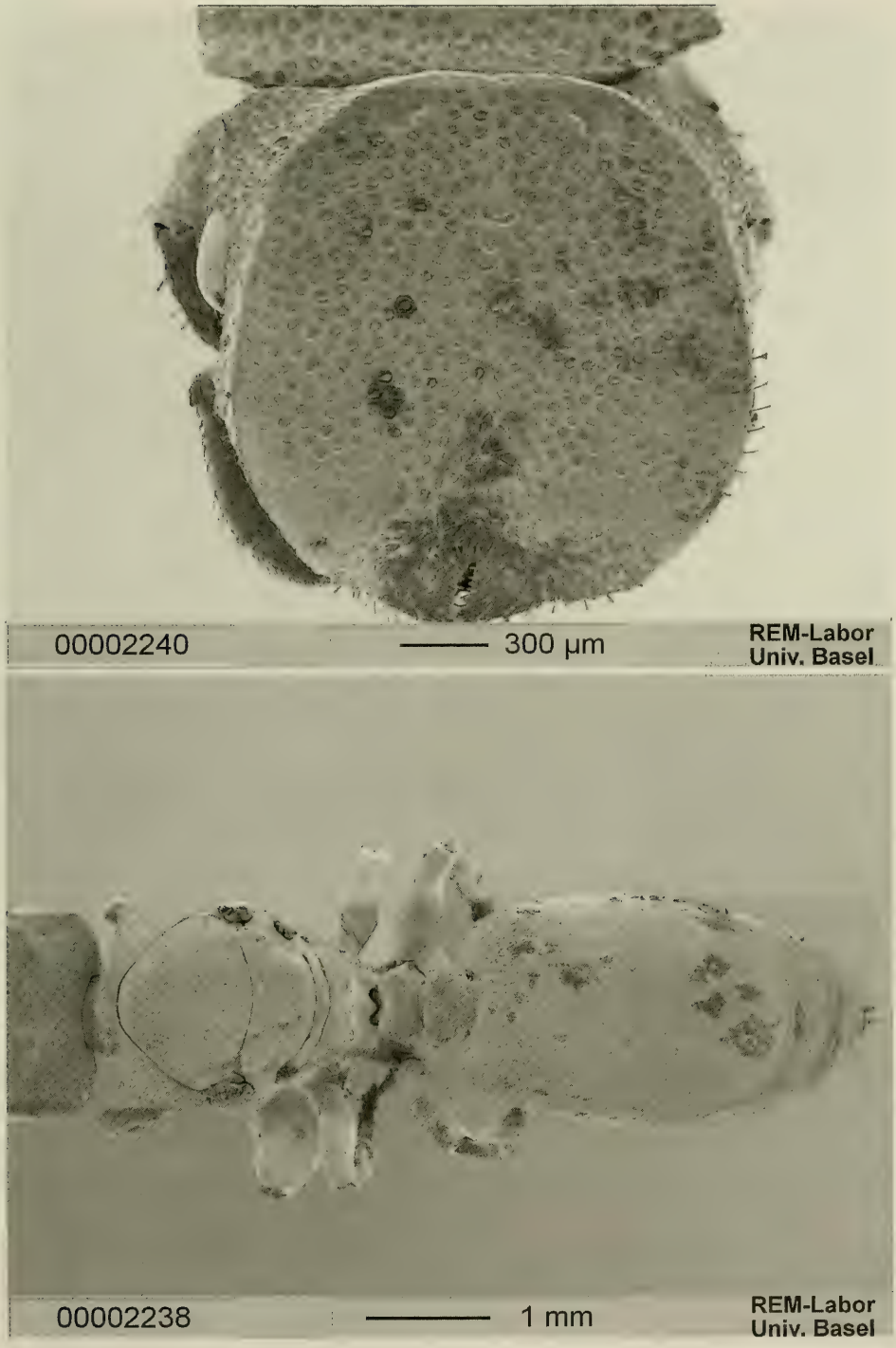


Fig. 277. *Cephalotes curvistriatus* (FOREL). Gyne intercepted in Miami, Florida: head (top) and meso- and metasoma (bottom) in dorsal view.

S o l d i e r (Fig. 276) (description of KEMPF, 1958 a). - "Total length 5.3–6.1 mm; maximum length of head 1.57–1.82 mm; maximum length of thorax 1.43–1.61 mm. Black; the following ferruginous: mandibles except chewing border, first funicular segment, apex of ultimate funicular segment, tarsites II - V; yellowish-brown: anterolateral portions of cephalic disc, tip of femora, extensor face of tibiae, gastral maculae.

Head somewhat shiny, surmounted by a subcircular, excavate disc, the floor of which is rather flat, the sides of which are strongly raised, concealing the floor of the disc, when head is seen in profile.

The lateral border of the cephalic disc, somewhat behind the eyes, curves abruptly more strongly mesad, forming an obtuse angle and joining the concave or convex occipital border at another angle, which is occasionally drawn out in the form of a very blunt tooth. Clypeal sutures vestigial. Floor of disc semitransparent above the antennal scrobe. Occipital lobes forming a more or less rounded corner, their posterior border strongly marginate. Floor of disc, sides of head and occiput finely yet superficially reticulate-punctate, covered with dense, somewhat larger, squamiferous foveolae, the intervals between the pits usually not exceeding, generally less than, the diameter of the pits. Lower face of head superficially reticulate, highly shining, sparsely foveolate.

Thorax subopaque. Anterior border arched mesially, slightly excised laterally; the anterior corner strongly dentate; the lateral border between this tooth and the strongly crested, raised, mesially broadly and shallowly interrupted transverse carina, is excised; following the carina strongly converging mesad, nearly straight. Promesonotal suture distinct. Mesonotum with a rounded or subangulate lobe on each side. Mesoepinotal suture impressed. Anterior corner of basal face of epinotum subdentate, followed posteriorly by a narrow, deep notch, and behind this notch a rather small, yet acute, tooth pointing obliquely cephalad, the posterior corner unarmed. Declivous face scarcely excavate discad, finely reticulate-punctate, with a few sparse longitudinal rugosities on its upper half, its lateral border marginate. Dorsum of thorax sculptured as head disc, except on the anteromesial portion of the basal face of epinotum where a few strong but very short longitudinal rugae are apparent. Sides of thorax opaque, finely reticulate-punctate, with occasional, rather irregular, rugosities. Fore coxae somewhat striate on the outer face. Femora fusiform.

Peduncular segments as in worker, but lacking the strong rugosities on dorsum, and the petiole small denticles on the upper border of the anterior face. Gaster similar to that of worker, the anterolateral hyaline crest very narrow or vestigial, not reaching back to the stigma of the first tergite. Longitudinal rugosities on first tergite very prominent on anterior third. Conversely the lateral rugosities or striae of the first sternite do not all, or just a few, converge concentrically and fuse mesially in front of the posterior border. Standing hair as in worker, a row of rather prominent setae around the border of the cephalic disc, reaching to backward beyond the eye, also a few laterally on the occipital lobe. Scalelike hair silvery, decumbent, in foveolae of head, thorax, peduncle. Cheeks and lower half of pleura very densely scaled. Scalelike hair small and very sparse on gaster, also sparse on lower face of head, sides of legs, and first sternite."

Measurements (in mm) and indices: TL 5.36–6.20; HL 1.40–1.62; HW 1.60–1.76; EL 0.32–0.36; PW 1.52–1.64; PeW 0.68; PpW 0.72–0.76; HBaL 0.48–0.52; HBaW 0.12–0.13; CI 108.6–114.3; PI 105.3–107.3; PPeI 223.5–241.2; PPpI 211.1–215.8; HBaI 25.0.

G y n e (Fig. 277) (description of KEMPF, 1958 a). - "Total length 7.2–7.5 mm; maximum length of head 1.75–1.78 mm; maximum length of thorax 2.10–2.14 mm. In general resembling the soldier, with the differences of the caste and the following noteworthy features.

Posterior third of cephalic disc not excavate, but slightly convex; the lateral borders not raised. Posterior pair of ocelli very close to the occipital border. Transverse pronotal crest sharply marginate, not as prominent as in soldier, broadly interrupted mesially, not quite attaining the lateral border of pronotum. Lateral border of basal face of epinotum with a blunt triangular lobe, and a similar very short tooth on the posterior corner. Lateral processes of peduncular segments very short, the postpetiole, as seen in profile, strongly convex above. Gaster relatively short and broad. Outer face of fore coxae with a few vestigial, oblique rugosities. First gastral sternite mostly smooth, finely striato-rugose anterolaterally, the striae

Fig. 278. *Cephalotes curvistriatus* (FOREL). Gyne intercepted in Miami, Florida, fore and hind wings.

not converging behind in front of the posterior border. Wings slightly infumated. Fore wing extending backwards slightly beyond the tip of the normally extended gaster, lacking a transverse cubital vein, the radial vein touching directly the cubital vein (r-m absent, according to the terminology of H. H. Ross)."

Wings (Fig. 278): fore wings with *R+Sc* connected to a marked pterostigma. *2r* marked, *Rsf5* connected with *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* almost absent. Hind wings with *R*, *M*, and distal half of *M+CuA* marked; proximal part of *M+CuA* and distal part of *M* and *CuA* vestigial to absent.

Measurements (in mm) and indices: TL 7.48–7.72; HL 1.60–1.64; HW 1.72; EL 0.36–0.37; PW 1.68; PeW 0.64–0.68; PpW 0.80; HBaL 0.60; HBaW 0.16; CI 104.9–107.5 PI 102.4; PPeI 247.0–262.5; PPpI 210.0; HBaI 26.7.

M a l e (Fig. 279) (previously undescribed). - Head (eyes included, mandibles excluded) 1/3 broader than long; vertexal angles strongly convex in full face view. Ocelli protuberant on the vertex. Eyes broadly convex and placed in the middle of the sides of the head. Frontal carinae diverging backwards and almost reaching the posterior border of the eyes. Frons flat. Clypeus convex, its anterior third flat. Mandibles slender, without lateral carina and with two distinct apical teeth. Scapes thick, twice longer than the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma. Pronotum in dorsal view broadening backwards. Mesonotum convex; median Mayrian carina and parapsidal furrows weakly impressed. Scutellum convex, its sides converging posteriorly. Propodeum with differentiate basal and declivous faces; basal face convex, its sides converging posteriorly.

Petiole as broad as the postpetiole; its dorsal face sloping into the concave anterior border; its sides convex anteriorly and converging posteriorly. Postpetiole slightly convex, with a pair of small denticles on the anterior half of its sides.

Gaster narrower than the mesosoma.

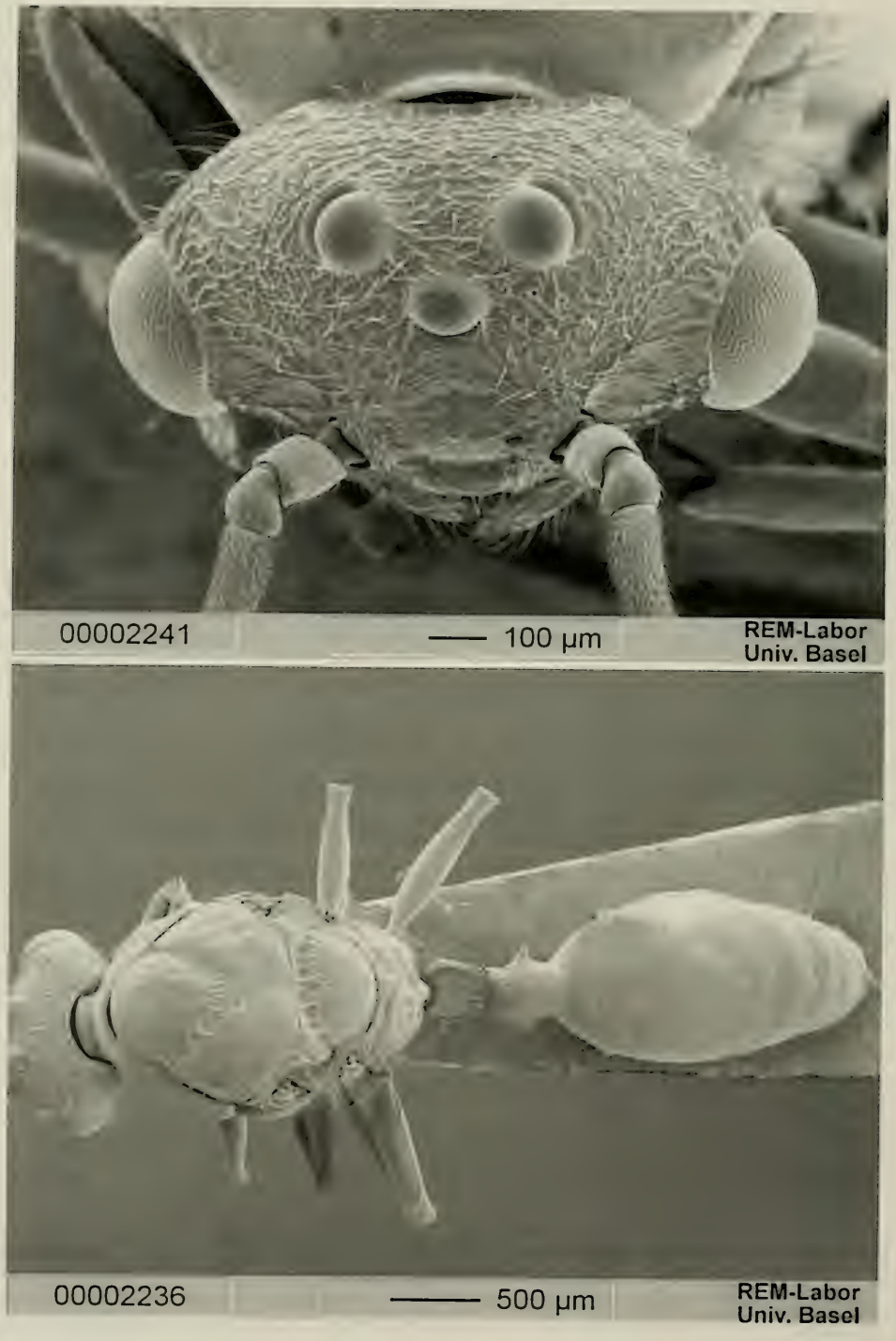


Fig. 279. *Cephalotes curvistriatus* (FOREL). Male from San José, Costa Rica: head (top) and meso- and metasoma (bottom) in dorsal view.

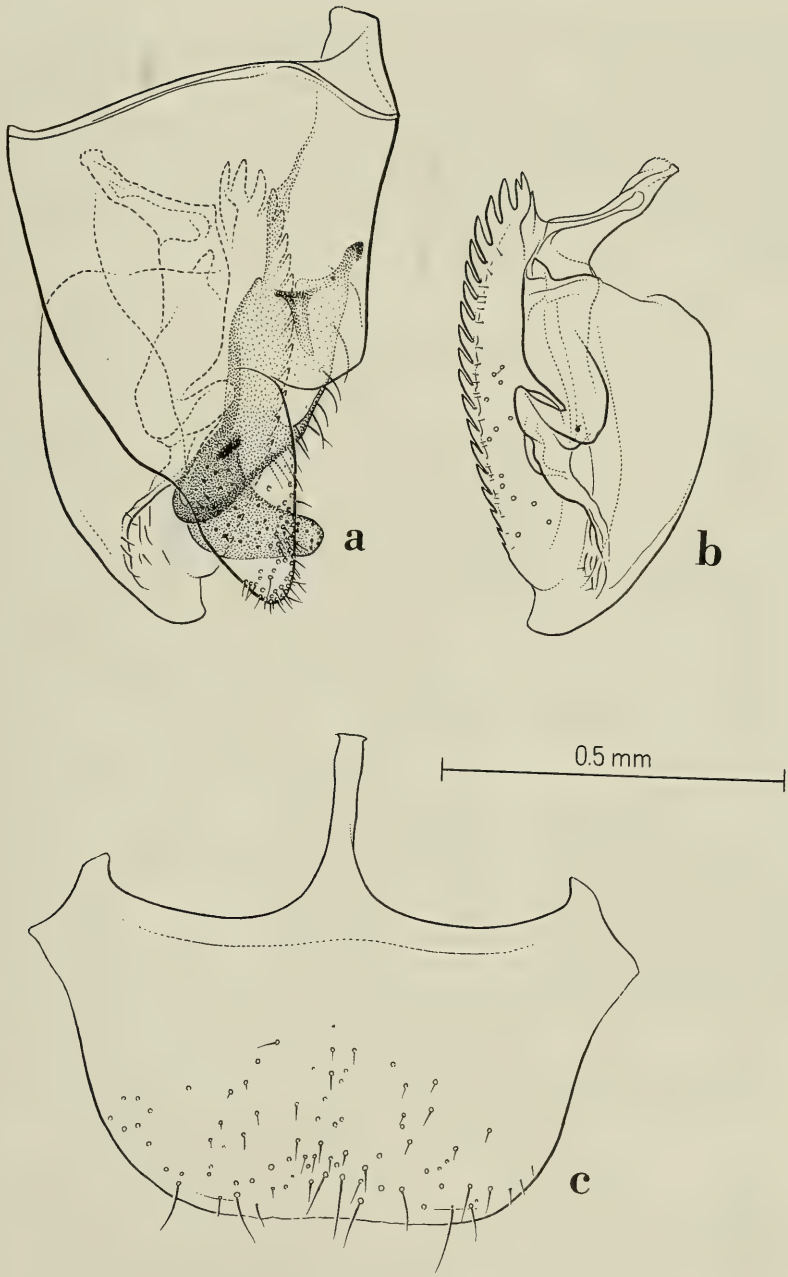


Fig. 280. *Cephalotes curvistriatus* (FOREL). Male from San José, Costa Rica. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Genitalia and subgenital plate as in Fig. 280.

Wings as in the gyne.

Sculpture. Head with thin, irregular anastomosing rugosities and punctated. Mesonotum, propodeum, petiole and sides of the thorax superficially and minutely reticulate-punctate and with irregular to almost longitudinal rugosities. Pronotum, postpetiole, and first gastral tergite reticulate-punctate; the same type of sculpture but more superficial on the legs, on the remaining tergites and on the sternites. Sparse and shallow, foveae-like, depressions the thorax.

Pilosity. Body covered by long, thin, dense, suberect and subdecumbent hairs; first gastral tergite and sternite, and dorsal half of femora with the same type of hairs but decumbent and shorter. Funiculi densely covered by thin, short, decumbent hairs; similar but thinner, sparser and slightly longer hairs on the legs.

Colour: head, mesosoma and pedicel brown; antennae, gaster and legs light brown.

Measurements (in mm) and indices: TL 4.92–5.14; HL 0.74–0.78; HW 0.96–1.00; EL 0.39–0.40; PW 1.04–1.08; PeW 0.35–0.39; PpW 0.41–0.43; HBaL 0.52–0.54; HBaW 0.08–0.09; CI 128.2–129.7; PI 92.3–92.6; PPeI 276.9–297.1; PPpI 241.9–263.4; HBaI 15.4–16.7.

Material examined. - All specimens collected in the U. S. from epiphytes of Costa Rican origin. **Costa Rica**: 27.XII.1935, *Cattleya dowiana* lot. no. 36.30, 8 workers 3 soldiers, 1 gyne [USNM]; 22.V.1940, *Cattleya* plants, 1 worker, 1 male [USNM]; 22.XII.1944, on pseudobulb of *Cattleya dowiana* (San Francisco), 5 workers, 2 soldiers, 1 gyne [USNM]; 02 & 11.VIII.1945, on orchid, pseudobulb (Brownsville, Texas), 1 worker, 4 soldiers, 1 gyne, 4 males [MCZC, MZSP, USNM]; 19.X.1945, on pseudobulb of *Cattleya dowiana* (Brownsville), 2 workers, 1 soldier, [USNM]; 11.VIII and 15.X.1945, on *Cattleya dowiana* (San Francisco, California), 6 workers, 1 soldier [MZSP, USNM]; 25.III, 08.V and 24.VI.1946, on pseudobulb of *Cattleya dowiana* (Brownsville, Texas), 4 workers, 1 soldier, 6 gynes, 3 males [MZSP, USNM]; 25–26.IV and 13.V.1946, on *Cattleya* pseudobulb (Hoboken, New Jersey), 22 workers, 2 soldiers, 1 gyne, [USNM]; San José, 02.VI and 01.X.1946, on *Cattleya dowiana* (San Francisco), 10 workers, 5 soldiers, 2 gynes, 1 male [USNM]; 11.VIII.1958, on orchids (Florida), 2 gynes [USNM].

Discussion. - This species has been not collected any more in its native area since its first collection by ANASTASIO ALFARO in 1899. The subsequent long list of interceptions on *Cattleya* of Costa Rican origin strengthens its natural homeland and suggests a probable symbiosis with orchids or, at least, with epiphytes. It has been recently recorded from The Netherlands as imported with epiphytes of the genus *Tillandsia* from Costa Rica (VIERBERGEN, 1994).

KEMPF (1958 a) reported *curvistriatus* also from Honduras and from Guatemala. The Honduran specimens will be described in this paper as a new species, *lenca* and the Guatemalan ones actually should be attributed to *sobrius*.

Distribution: Costa Rica.

Cephalotes sobrius (KEMPF) new combination
Figs. 281, 282, 283, 284

Paracryptocerus sobrius KEMPF, 1958 a: 119, pl. 4, fig. 6, pl. 5, fig. 6, pl. 6, fig. 1. Soldier and gyne. Original description. Type locality: intercepted by the U. S. Plant Quarantine inspectors in New Jersey on *Epidendrum aromaticum* imported from Guatemala. Type material: holotype soldier and 5 paratype gynes (MZSP), examined.

Paracryptocerus curvistriatus (FOREL), KEMPF, 1958 a: 118. Worker. Partim. Misidentification.

Zacryptocerus sobrius, HESPENHEIDE, 1986: 395. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *texanus* clade differing from its sister species, *lenca*, by the absence of thick longitudinal rugosities on the posterior face of the femora of the worker.

W o r k e r (Fig. 281). - Head subquadrate. Vertexal angles round, with weakly crenulate borders. Vertexal margin gently concave. Cheeks marginate above and below Frontal carinae upturned over the eyes. Mandibles laterally carinate.

Mesosoma almost flat in side view. Pronotum in dorsal view with the anterior border convex. Scapular angles absent or not visible in dorsal view. Pronotal sides with a narrow lamella with three pairs of teeth, the anterior pair short, pointed, and slightly direct anteriorly, the second pair similar in size to the first, and the third almost round. Sides of mesonotum with a pair of minute denticles. Promesonotal suture superficially impressed. Propodeal suture marked. Propodeum with differentiate basal and declivous faces; basal face narrowing backwards, with three or four pairs of teeth, the second pair larger than the others, the third and fourth pairs minute, rarely absent in some specimens; declivous face converging posteriorly.

Petiole anteriorly truncate; its anterior border marked by a pair of small denticles. Petiolar spines slightly shorter than the petiole, thin, pointed backwards and originating from the beginning of the petiolar sides. Postpetiole broader than petiole, with thin, pointed spines arising anterolaterally and curved backwards. Postpetiolar dorsum gently pointed dorsally.

Gaster oval, with an antero lateral crest not surpassing the first gastral stigma backwards.

Mid and hind femora angulate; mid and hind basitarsi long and without flat and broad base.

Sculpture. Head dorsum superficially and minutely punctate, with foveae deep and broader than their interspaces, diminishing in size anteriorly. Frontal carinae superficially punctate and with sparse, faint foveae and few, thin, oblique rugosities. Ventral face of the head and sides of the mesosoma superficially punctate and with thick longitudinal striae, the striae less regular on the pleurae. Mesosoma superficially punctate, with thick, longitudinal striae, rarely irregular. Pedicel with the same sculpture as the mesosoma but more irregular and with few, irregular foveae.

First gastral tergite superficially and minutely reticulate, with thin, irregular, longitudinal rugosities. First sternite with longitudinal rugae on the sides and on the anterior half; posterior half of the first gastral sternite superficially punctate and shining.

Legs reticulate-punctate, with slightly shining anterior and posterior faces of the femora. Distal part of the outer face of the femora and outer face of tibiae covered by small, irregular, superficial foveae.

Pilosity. Body with five types of hairs: (1) appressed and thick originating from each fovea; many more similar but originating or not from foveae thinner and sparse on the mesosoma and on the pedicel, dense on the cheeks, on the mesopleurae, on the middle of the metapleurae, on the gaster, on the distal part of the outer face of the femora and on the outer face of tibiae; (2) slightly clubbed on the sides of the frontal carinae, of the mesosoma, of the pedicel, on the anterolateral border of the first tergite, and on the legs; (3) truncate and subdecumbent, as long as the clubbed ones, mixed with type (1) hairs, on the pedicel and on the gaster; (4) minute and thin on the first gastral sternite; (5) long and slightly pointed on the posterior border of the gastral sternites.

Colour. Dark brown. Frontal carinae, tibiae, tarsomeres, mesosomal and peduncular spines yellowish-orange. First gastral tergite with a pair of yellow, oval spots anterolaterally. Anterolateral crest of the first gastral tergite yellowish-transparent.

Measurements (in mm) and indices: TL 3.92–4.68; HL 0.96–1.12; HW 1.12–1.24; EL 0.28–0.31; PW 1.06–1.08; PeW 0.56–0.62; PpW 0.65–0.742; HBaL 0.40–0.44; HBaW 0.08–0.09; CI 110.7–116.7; PI 112.0–114.8; PPeI 174.2–178.6; PPpI 145.9–153.8; HBaI 20.0–20.4.

S o l d i e r (Fig. 282) (description of Kempf, 1958a). - "Total length 6.3 mm; maximum length of head 1.85 mm; maximum width of cephalic disc 1.86 mm; maximum length of thorax 1.68 mm; maximum width of thorax 1.71 mm. Black; the following fuscous ferruginous: mandibles, anterolateral portions of cephalic disc, tip of scape, tibiae, tarsi, tip of peduncular spines; anterolateral corners of gaster with a yellowish-brown spot.

Head subopaque, subquadrate, surmounted by a nearly circular, anterolaterally somewhat excavate, mesially slightly convex, posteriorly nearly flat disc, the borders of which are noticeably crenulate but distinctly upturned laterally, more noticeably crenulate but not

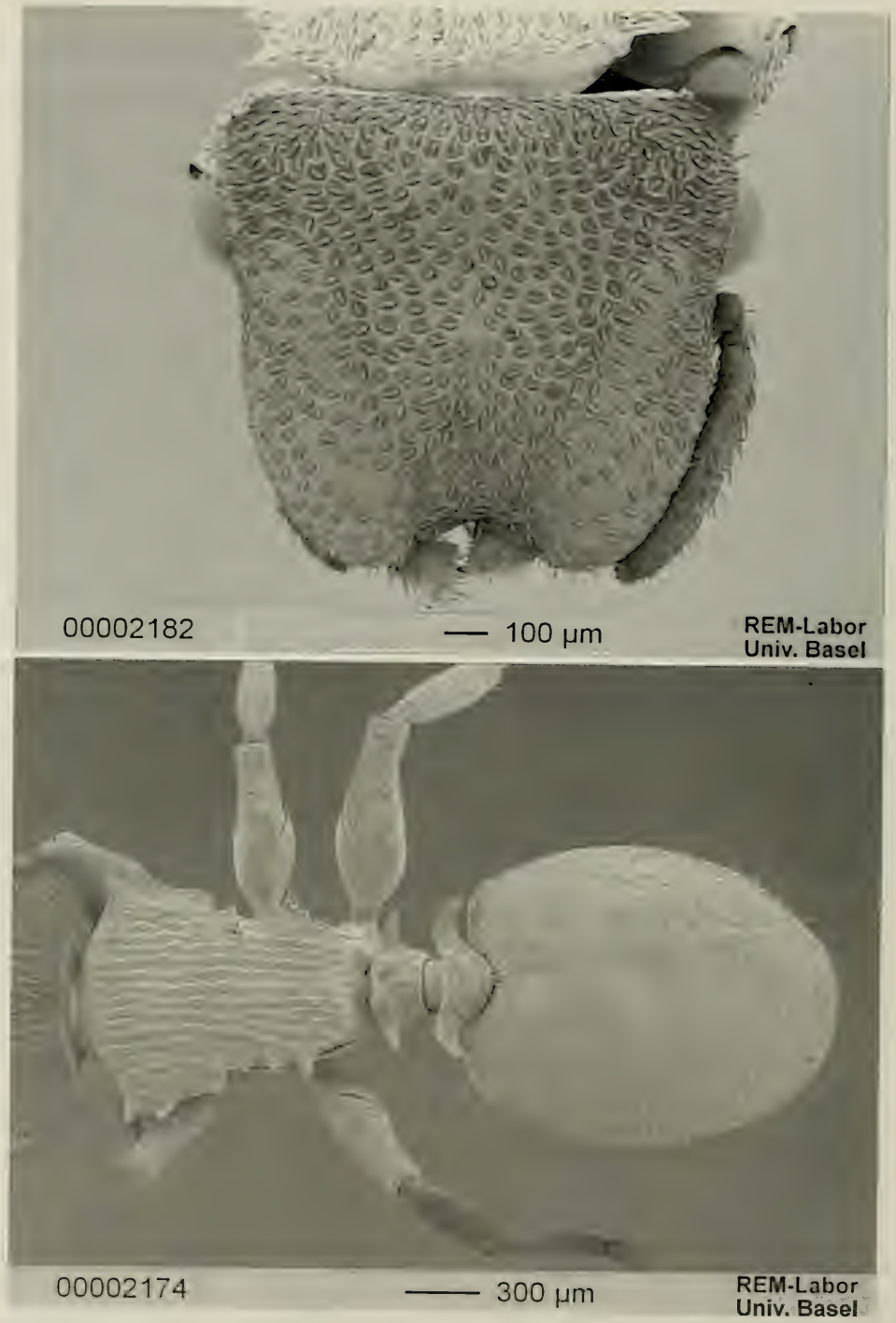


Fig. 281. *Cephalotes sobrius* (Kempf). Worker from Guatemala (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

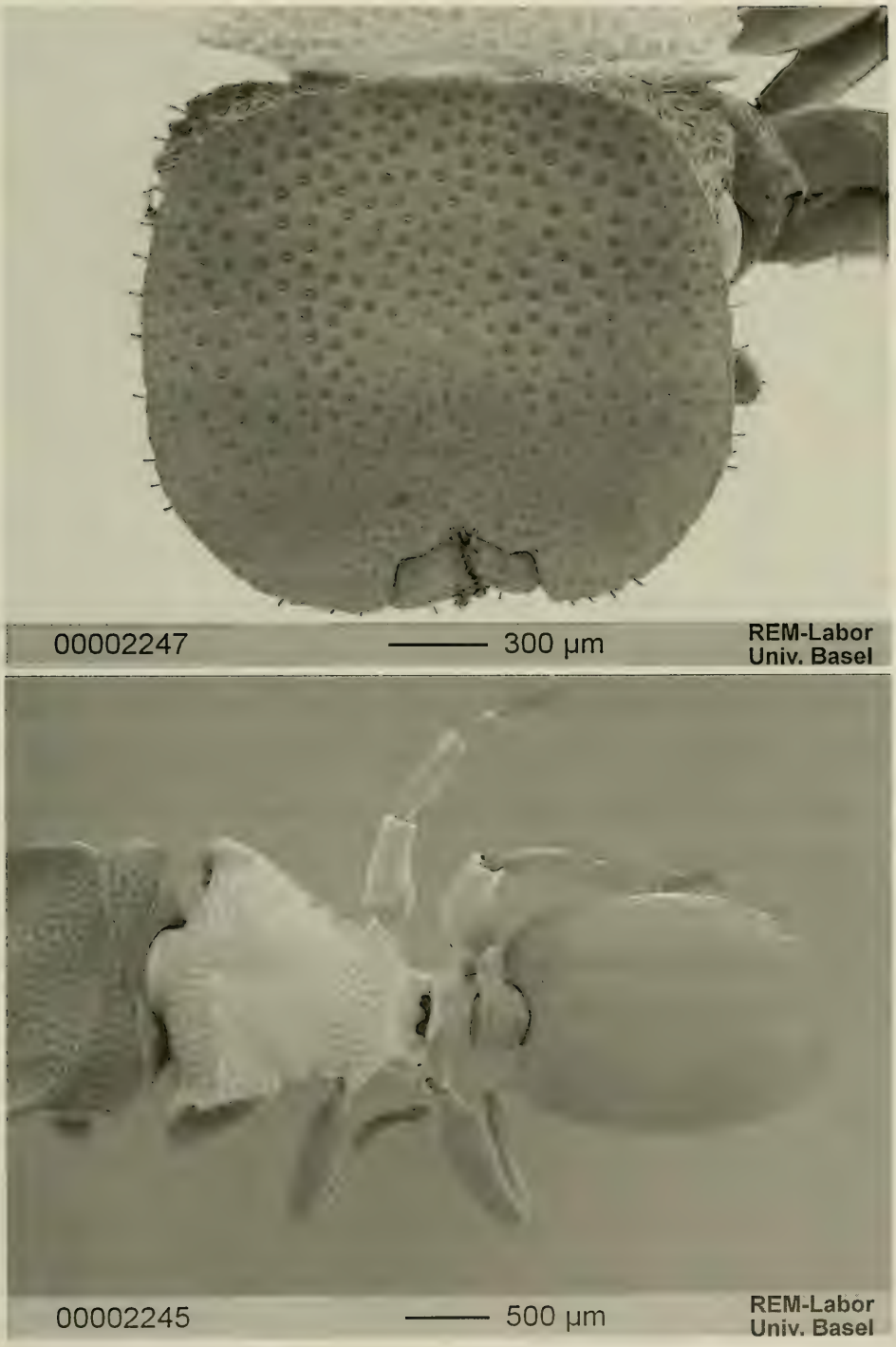


Fig. 282. *Cephalotes sobrius* (KEMPF). Soldier from Guatemala (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

upturned posteriorly. Median portion of posterior border of cephalic disc vestigially excised or truncate between the vestigial, scarcely noticeable, occipital denticles. Floor of disc scarcely visible when head is seen in profile. Borders of occipital lobes sharply marginate, the lateral border crenulate, visible from the side as a distinct carina which runs foreward and upward on the sides of head toward the upper border of eye, but fading out before reaching it. Floor of disc finely but superficially reticulate-punctate, with sparse, larger foveolae, the interval between the foveolae being usually as broad, or even much broader than, the diameter of the pits. Foveolae larger, slightly more crowded on the sides of head and occiput. Lower face of head very finely reticulate-punctate, very sparsely foveolate.

Thorax opaque, finely reticulate-punctate throughout. Anterior border convex mesially, slightly concave laterally. Anterior corner with a prominent tooth. Lateral border of pronotum subparallel, crenulate, in front of the transverse carina, straight, converging caudad behind the carina, the posterior corner separated by mesonotum by a deep and narrow excision. Transverse pronotal carina not conspicuously crenate, sharply marginate, moderately prominent, shallowly excised medially. Promesonotal suture vestigial. Lateral lobes of mesonotum obliquely truncate and marginate. Mesoepinotal suture impressed laterally, vestigial mesially. Anterior corner of basal face of epinotum subrectangular, vestigially denticulate, followed behind by a broader, triangular projecting lobe, the posterior corner at most slightly dentate, practically unarmed. Declivous face not excavate, its lateral borders submarginate. Foveolae on dorsum of thorax slightly larger, and more crowded than on head disc, densely crowded on posterior half of basal face of epinotum, where the integument becomes reticulate-rugose. Sides of thorax with occasional irregular rugosities and grooves. Fore coxae with vestigial, fine, oblique rugulae on apical half of the outer face.

Peduncular segments opaque. Foveolae very dense, and irregular in shape. Postpetiole broader than petiole, the latter on each side with a strong, obliquely reflexed spine, the spine itself not curved. Anterior face of petiole obliquely truncate, bearing on the upper marginate border two minute denticles. Postpetiole with conspicuously longer, rather delicate lateral processes, the tip of which is obliquely recurved caudad. Body of postpetiole, as seen in profile, convex, the deepest portion just a little behind the anterior border.

Gaster opaque, subovoid. Anterior border moderately excised mesially, very narrowly crested laterally. First tergite finely reticulate-punctate, with slightly larger, yet very fine, rugosities, which form a scarcely raised network between the slightly impressed piligerous punctures. First sternite with a smooth posteromedian area, which is shiny, the rest subopaque, finely reticulate-punctate, with very fine longitudinal rugosities on the sides.

Standing hair thick, obtuse on apex, around the rim of cephalic disc, up to the posterior border, on the lateral border of occipital lobes, on the anterior half of the border of pronotum, one or two on mesonotal lobes, tip of peduncular spines, and a few on the anterolateral gastral crests and along the posterior border of the gastral sternites and tergites, and sparsely on the posterior half of the first sternite. Decumbent hairs scalelike, silvery, canaliculate, rather short in all foveolae of the head, thorax and peduncle. Very conspicuous on mesopleura where they are largest. very fine and minute on the first gastral tergite. Rather dense on the extensor faces of femora and tibiae."

Measurements (in mm) and indices: TL 5.72–6.44; HL 1.48–1.60; HW 1.64–1.80; EL 0.32–0.36; PW 1.56–1.76; PeW 0.72–0.76; PpW 0.84–0.92; HBaL 0.33–0.48; HBaW 0.11–0.12; CI 110.8–112.5; PI 102.3–105.1; PPeI 216.7–231.6; PPpI 185.7–191.3; HBaI 25.0–26.2.

G y n e (Fig. 283) (description of KEMPF, 1958a). - "Total length 6.5–6.8 mm; maximum length of head 1.57–1.64 mm; maximum width of cephalic disc 1.46–1.50 mm; maximum length of thorax 1.89 mm; maximum width of thorax 1.43–1.50 mm. In general resembling the soldier, with the peculiarities of the caste.

Cephalic disc more elongate, the floor mostly convex, only the anterolateral portions being slightly excavated. Anterolateral borders of disc slightly raised. Posterior half of disc either trapezoidal or more or less rounded. Posterior pair of ocelli very close to the occipital border. Lower face of head with the foveolae slightly larger and denser, and occasional longitudinal grooves. Occipital lobes with scarcely crenate border, the posterior corner rounded. Ante-

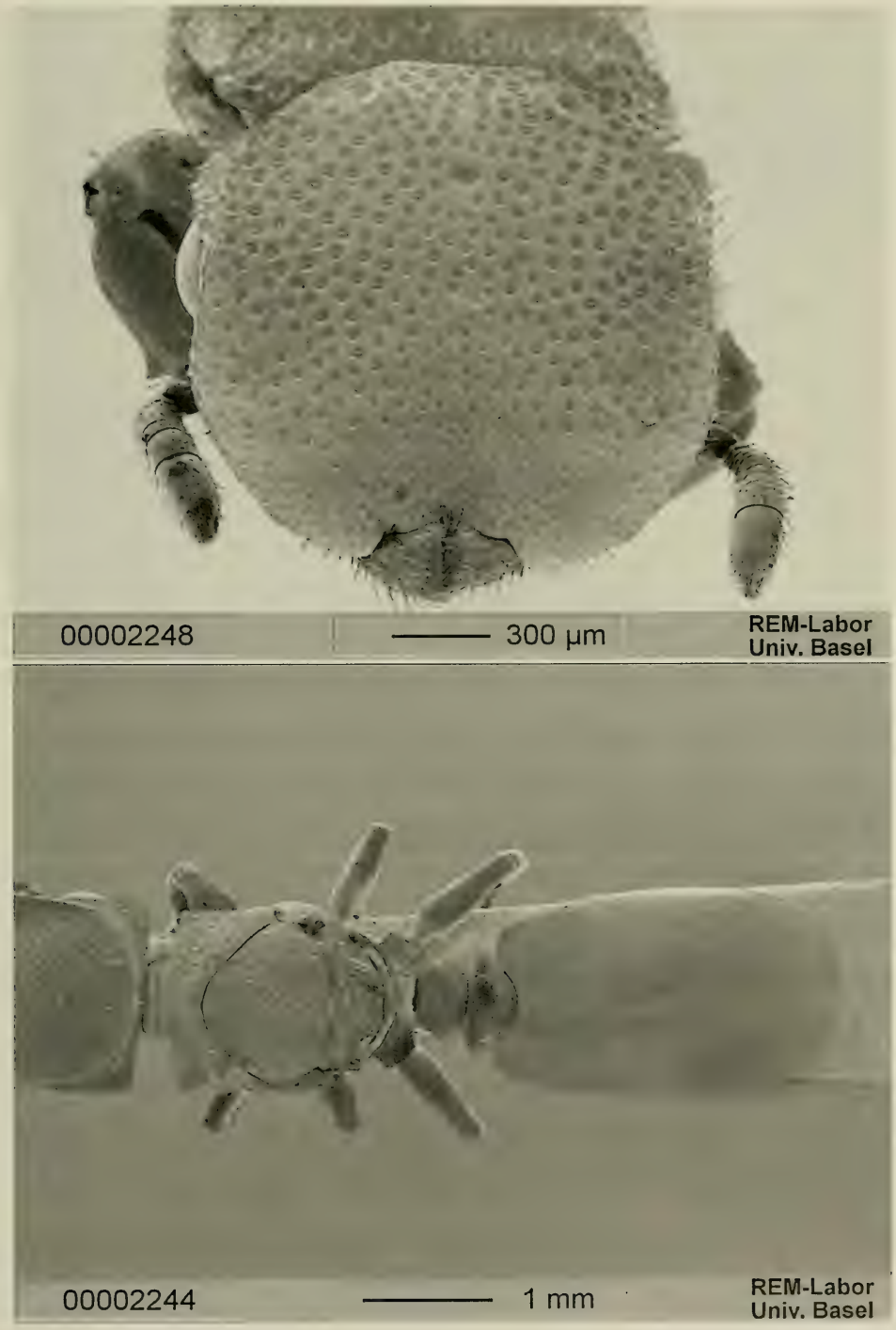


Fig. 283. *Cephalotes sobrius* (KEMPF). Gyne from Guatemala (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

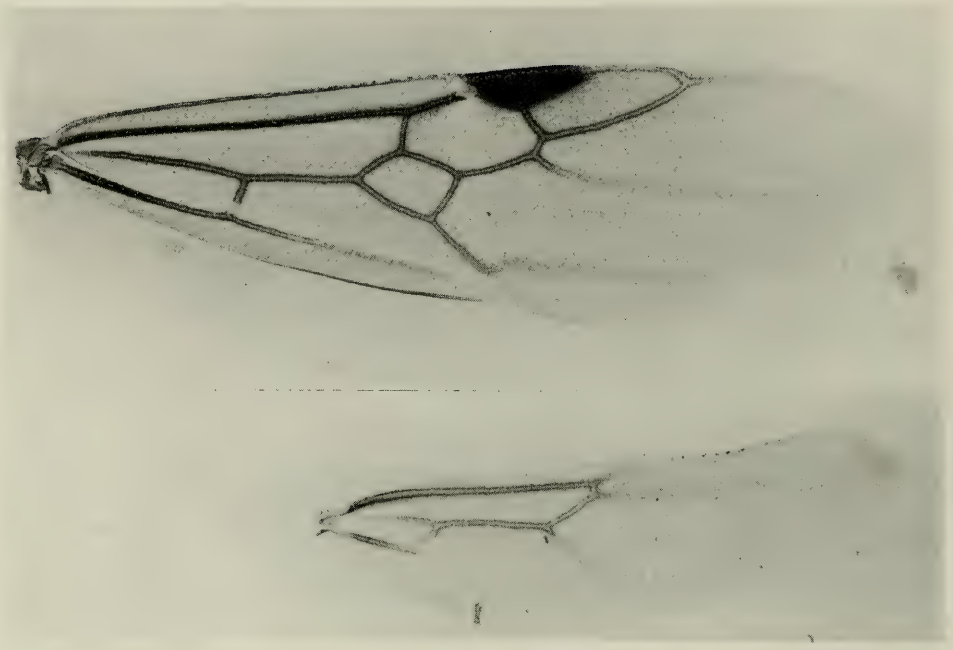


Fig. 284. *Cephalotes sobrius* (Kempf). Gyne from Guatemala (no further locality), fore and hind wings.

rior corner of thorax dentate, the tooth not very prominent. Transverse pronotal carina little raised, vestigial toward the lateral border of pronotum, shallowly excised mesially. Lateral border of basal face of epinotum with a triangular lobe, the posterior corner unarmed, the posterior border nearly straight and transverse. Scutum very sparsely foveolate, the pits being somewhat denser on pronotum and scutellum, very dense and crowded on basal face of epinotum. Declivous face not excavate, its lateral borders immarginate. Mesopleural tooth prominent. Fore coxae with oblique rather coarse rugosities toward apex, of outer side. Petiole with obliquely truncate anterior face, the upper border of which is sharply marginate, forming with the dorsal face, as seen in profile a subacute angle. Lateral tooth of petiole relatively strong and projecting. Postpetiole with the same, yet shorter, rather delicate, more or less straight, lateral processes as in soldier. In profile the dorsum of this segment forms an anterior steeply ascending face, and a posterior descending face, meeting at an acute angle, the deepest part of the segment being farther removed from the anterior border, nearly in the middle of the length of the segment. Gaster subcylindrical, dotted with pale-yellowish on the anterior corner, and bearing on each anterolateral lobe a very narrow thin crest. Wings nearly hyaline, the pterostigma almost black, the veins brown. Venation of fore wing normal, transverse cubital vein (or vein: *r-m*) present. Fore wing, when reflexed backwards extending well beyond the normally contracted gaster."

Wings as in Fig. 284.

Measurements (in mm) and indices: TL 6.56–7.08; HL 1.40–1.52; HW 1.40–1.52; EL 0.33–0.36; PW 1.32–1.40; PeW 0.68–0.72; PpW 0.84–0.88; HBaL 0.48–0.56; HBaW 0.11–0.13; CI 100.0; PI 106.1–109.1; PPeI 183.3–194.4; PPpI 150.0–159.1; HBaI 22.9–23.2.

Material examined. - **Guatemala**: 14.V.1946, 1 soldier (holotype), 5 gynes (paratypes) (intercepted by U. S. Plant Quarantine Inspectors at Hoboken, N. J., n. 46–8236, on imported pseudobulbs of *Epidendrum aromaticum* from Guatemala) [MZSP]; same data

and equally belonging to the type-series, although not labelled as such, 7 workers, 19 soldiers, 11 gynes [USNM, MZSP].

Discussion. - KEMPF (1958a) described *C. sobrius* on the basis of soldiers and gynes only. He considered the workers associated with these soldiers and gynes as belonging to *C. curvistriatus* and explained his conclusion by means of a hypothetical mixture of material during the collecting or during the labelling. At first glance his idea is tempting since the workers in question are very similar to those of *curvistriatus*, but a careful examination shows that they differ from *curvistriatus* by the following characters: vertexal margin gently concave (deeply concave in *curvistriatus*), hind and mid femora angulate (without angle or denticle in *curvistriatus*), longer peduncular spines, striae thicker on the ventral part of the head and thinner on the first gastral sternite. *Sobrius*, in our cladogram, is closer to *lenca* (q. v.) than to *curvistriatus*. The workers of *sobrius*, *lenca* and *curvistriatus* are characterised by the thick striae on the mesosoma and on the ventral part of the head. The worker of *C. sobrius* shares with *lenca* the angulate hind and mid femora. The soldiers of *sobrius* and *curvistriatus* share the floor of the disc not deeply concave, the basal face of the propodeum with irregular denticles, the yellow spot on first gastral tergite, and the anterior fourth of the tergite with longitudinal, irregular rugosities.

Distribution: presumably Guatemala.

Cephalotes lenca DE ANDRADE new species
Fig. 285

Paracryptocerus curvistriatus (FOREL), KEMPF, 1958 a: 118. Worker. Partim. Misidentification.

Holotype: worker intercepted by U. S. Plant Quarantine Inspectors at Hoboken, N. J., 19.V.1941, on *Cattleya* sp. from Honduras, n. 41–8337 (USNM).
Paratypes: 2 workers, same data as the holotype (USNM).

Derivatio nominis: this species is named after the Lenca, the Indians from Honduras.

Diagnosis. - A member of the *texanus* clade, the apomorphy of which is the thick longitudinal rugosity on the posterior face of the femora, a character uniquely derived for *lenca* in this clade. Other characters useful to recognise *lenca* are the thick striae on the ventral part of the head and on the sides of the first gastral sternite and the angulate mid and hind femora.

Worker (Fig. 285). - Head subquadrate. Vertexal angles round, with superficially crenulate borders. Vertexal margin gently concave. Cheeks marginate above and below. Frontal carinae with minute crenulations and upturned over the eyes. Mandibles laterally carinate.

Mesosoma convex in side view. Pronotum in dorsal view with the anterior border convex. Scapular angles absent. Humeral angles with three small pairs of teeth, the anterior pair pointed and directed laterally, the second pair similar in size to the first, and the third pair minute and variably pointed. Sides of mesonotum with a pair of teeth. Promesonotal and propodeal sutures superficially impressed. Propodeum with differentiate basal and declivous faces; basal face not strongly narrowing backwards, with three pairs of teeth, the second pair larger than the others, the third pair thinner, sometimes one additional pair of minute denticles are present between the second and third pairs of teeth; declivous face converging posteriorly.

Petiole anteriorly truncate; its anterior border bearing a pair of small denticles. Petiolar spines slightly shorter than the petiole, thin, pointed backwards and originating from the beginning of the petiolar sides. Postpetiole broader than petiole, with thin, pointed spines arising anterolaterally and gently curved backwards.

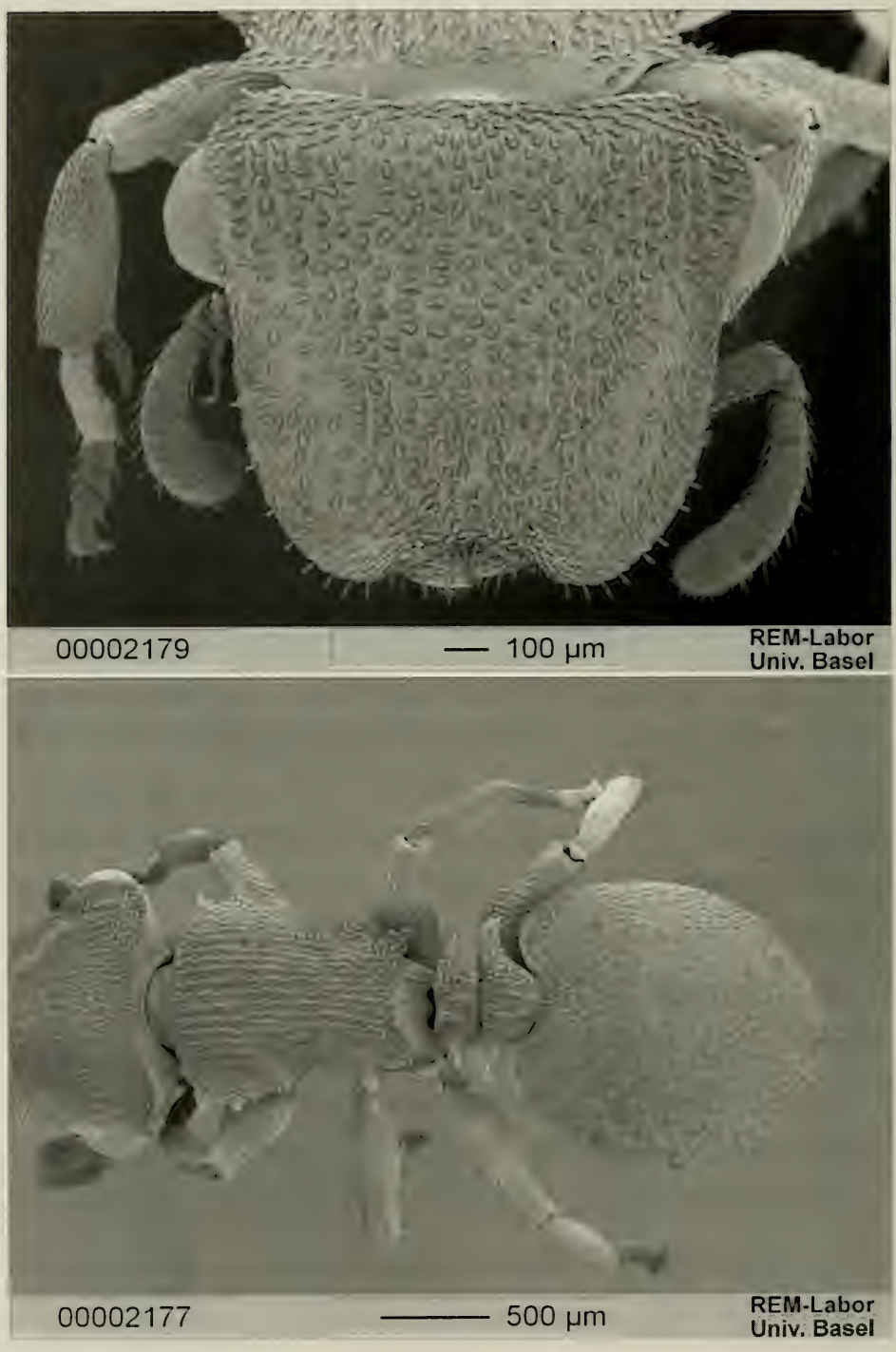


Fig. 285. *Cephalotes lenca* DE ANDRADE. Worker from Honduras (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Gaster suboval, with an anterolateral crest not surpassing the first gastral stigma backwards.

Mid and hind femora angulate; mid and hind basitarsi long and without flat and broad base.

Sculpture. Head dorsum superficially and minutely punctate, with anastomosing foveae forming longitudinal, irregular rugosities with their interspaces. Frontal carinae superficially punctate, with sparse, faint foveae and few, thin, longitudinal rugosities. Ventral face of the head and mesosoma superficially punctate and with thick longitudinal striae. Pedicel with the same sculpture as the mesosoma but more irregular.

First gastral tergite superficially and minutely reticulate, with irregular, longitudinal rugosities. First sternite with longitudinal striae on the sides and on the anterior half; its posterior half superficially punctate and shining.

Legs reticulate-punctate, with thick, longitudinal rugosities on the posterior face of the femora.

Pilosity. Body with five types of hairs: (1) appressed and thick originating from each fovea; many more, similar but not originating from foveae, dense on the mesosoma, on the pedicel, on the cheeks, on the mesopleurae, on the middle of the metapleurae, on the distal part of the extensor face of the femora and on the extensor face of tibiae, on the gaster but thinner; (2) slightly clubbed, on the sides of the frontal carinae, of the mesosoma, of the pedicel, on the anterolateral border of the first tergite, and on the legs; (3) truncate and subdecumbent, as long as the clubbed ones, mixed to type (1) hairs, on the pedicel and on the gaster; (4) minute and thin on the first gastral sternite; (5) long and slightly pointed on the posterior border of the gastral sternites.

Colour. Dark brown. Frontal carinae, tibiae, tarsomeres, mesosomal and peduncular spines yellowish-orange; basitarsi darker. First gastral tergite with a pair of yellow, oval spots anterolaterally. Anterolateral crest of the first gastral tergite yellowish-transparent.

Measurements (in mm) and indices: TL 3.70–4.16; HL 0.92–1.00; HW 1.04–1.16; EL 0.28–0.33; PW 0.90–1.04; PeW 0.57–0.63; PpW 0.74–0.75; HBaL 0.31–0.36; HBaW 0.08–0.09; CI 113.0–116.0; PI 111.5–115.5; PPeI 157.9–165.1; PPpI 121.6–138.7; HBaI 25.0–25.8.

Material examined. - **Honduras**: no further locality, intercepted by U. S. Plant Quarantine Inspectors at Hoboken, N. J., on *Cattleya* sp., 19.V.1941, n. 41–8337, 3 workers (holotype and paratypes) [USNM].

Discussion. - KEMPF (1958a) considered the specimens on which this species is based as belonging to *curvistriatus*, due to their superficial similarity with the latter. The two, however, differ by the mesosomal striation, much thinner in *lenca*, by the shape of the cephalic hairs, broader in *lenca*, and by the postpetiolar spines, shorter in *lenca*. As we already wrote under *sobrius*, the latter and not *curvistriatus* appears to be the sister species of *lenca*. *Lenca* differs from *sobrius* mainly by the presence of thick, longitudinal rugosities on the posterior face of the femora. The three species, however, are very similar each other and additional characters useful for their distinction have been already given in the discussion of *sobrius*.

Distribution: Honduras.

Cephalotes chacmul SNELLING new species

Figs. 286, 287

Type material: Holotype soldier from Reserva Sian Ka'an, km 11, Sabana, (Quintana Roo, Mexico) 3–4 June 1986, A. DEJEAN, from pseudobulbs of *Tillandsia balbiciana* (Bromeliaceae) (LACM); paratypes four soldiers and nine workers, same data as the holotype, three paratypes deposited in MCZC, three in BMNH and the remaining nine in LACM.

Derivatio nominis: *Chacmul* is the name of the Mayan jaguar god used here as specific name in apposition.

D i a g n o s i s . - A member of the *texanus* clade differing from its sister species, *auriger*, by the thin, appressed hairs on the first gastral tergite of the worker.

W o r k e r (Fig. 286) (description by R. R. SNELLING, personal communication). - "Measurements (mm): HW (greatest head width below the eyes) 0.84 - 0.89, HL (greatest length from the lower margin of the frontal lobes to the highest level of the margin of the vertex) 1.03–1.06, TL 3.4–4.0.

Head. About 1.2 times longer than broad. Lateral margins slightly divergent above, distinctly reflexed adjacent to eyes; dorsolaterad corners elevated and more or less crenulate; vertexal margin thin and cariniform, very weakly concave in frontal view. Front of head gently convex, with irregularly spaced fine foveolae and with fine, widely spaced longitudinal rugulae, especially across vertex and along sides. Gena and gulae area dull and with coarse longitudinal rugae. Foveae each with appressed, glittering scale-like seta; margins of head with short, erect, simple setae.

Mesosoma. Anterior margin of pronotal disc nearly straight; humeral angle distinct; side with three distinct spines, posterior spine shorter and with apex bluntly rounded or truncate. Mesoscutum with short, acute spine at side. Side of basal face of propodeum with three spines of variable length, mid spine sometimes bluntly rounded. Entire dorsum dull and with relatively coarse longitudinal rugae (partially replaced at sides by elongate setose foveae) that extend onto posterior slope of propodeum. Side of pronotum with curved longitudinal rugae on upper two-thirds or more; remainder of pronotal side irregularly roughened; mesepisternum and side of propodeum with much finer, irregular, longitudinal rugulae. Legs as in major.

Petiole with vertical anterior face, its summit cariniform and with two short submedian teeth; dorsal face with coarse, irregularly longitudinal setose foveae; lateral spines narrow and acute, slightly curved distad. Postpetiole disc with coarse elongate setose foveae; lateral spines similar to those of petiole but slightly broader and longer.

Metasomal tergum 1 invaginated at postpetiolar attachment and distinctly marginate anterolaterally, corner narrowly lamelliform. Disc of tergum 1 dull, weakly striate and with scattered setose foveae; sternum 1 dull, distinctly longitudinally striate at sides, middle one-third to one-half smooth and shiny.

Color blackish, appendages dark brownish; frontal lobes and mesosomal spines translucent yellowish; tibiae and tarsi reddish to yellowish; tergum 1 with anterolateral yellow spots."

Measurements (in mm) and indices: TL 3.28–4.24; HL 0.84–0.96; HW 0.88–1.04; EL 0.24–0.28; PW 0.78–0.96; PeW 0.46–0.56; PpW 0.52–0.64; HBaL 0.30–0.35; HBaW 0.07–0.09; CI 104.7–108.3; PI 108.3–112.8; PPeI 169.5–171.4; PPpI 150.0; HBaI 23.3–25.7.

S o l d i e r (Fig. 287) (description by R. R. SNELLING, personal communication). - "Measurements (mm): HW [greatest head width below the eyes] 1.48 (holotype), 1.48–1.55 (paratypes), HL (greatest length from the lower margin of the frontal lobes to the highest level of the margin of the vertex) 1.52 (holotype), 1.52–1.61 (paratypes), TL 5.2 (holotype), 4.9–5.4 (paratypes).

Head with complete frontal shield, about 1.05 (1.02–1.04) times as long as wide; margins of shield more strongly reflexed at sides, nearly straight across mid one-third of vertexal margin; dorsolateral corners of head thin and slightly reflexed, clearly visible in anterior view. Foveae of disc about 0.03 - 0.05 mm diameter, mostly separated by less than one-half fovea diameter, but with some interspaces greater than fovea diameter; interspaces slightly shiny and with numerous micropunctures, each fovea with one appressed, glittering scale-like seta that does not extend beyond fovea margin. Lateral margins of disc with sparse, short, erect, subspatulate setae; similar, but slightly longer, setae present along margins of posterolateral corners. Gular surface shiny between sparse foveae, each with glittering scale-like seta.

Mesosoma. Transverse pronotal carina distinct, somewhat irregular, broadly interrupted in middle; pronotal humerus absent; scapular angle acute; side of pronotal margin, in dorsal view, slightly sinuate and convergent distad, reentrant angle broadly rounded. Side of mesoscutum distinctly projecting as short, rounded lobe. Side of dorsal face of propodeum with short basal tooth; long, slightly curved blunt spine at midlength, and blunt posterior tooth. Dorsal face of propodeum short and abruptly rounded into posterior face.

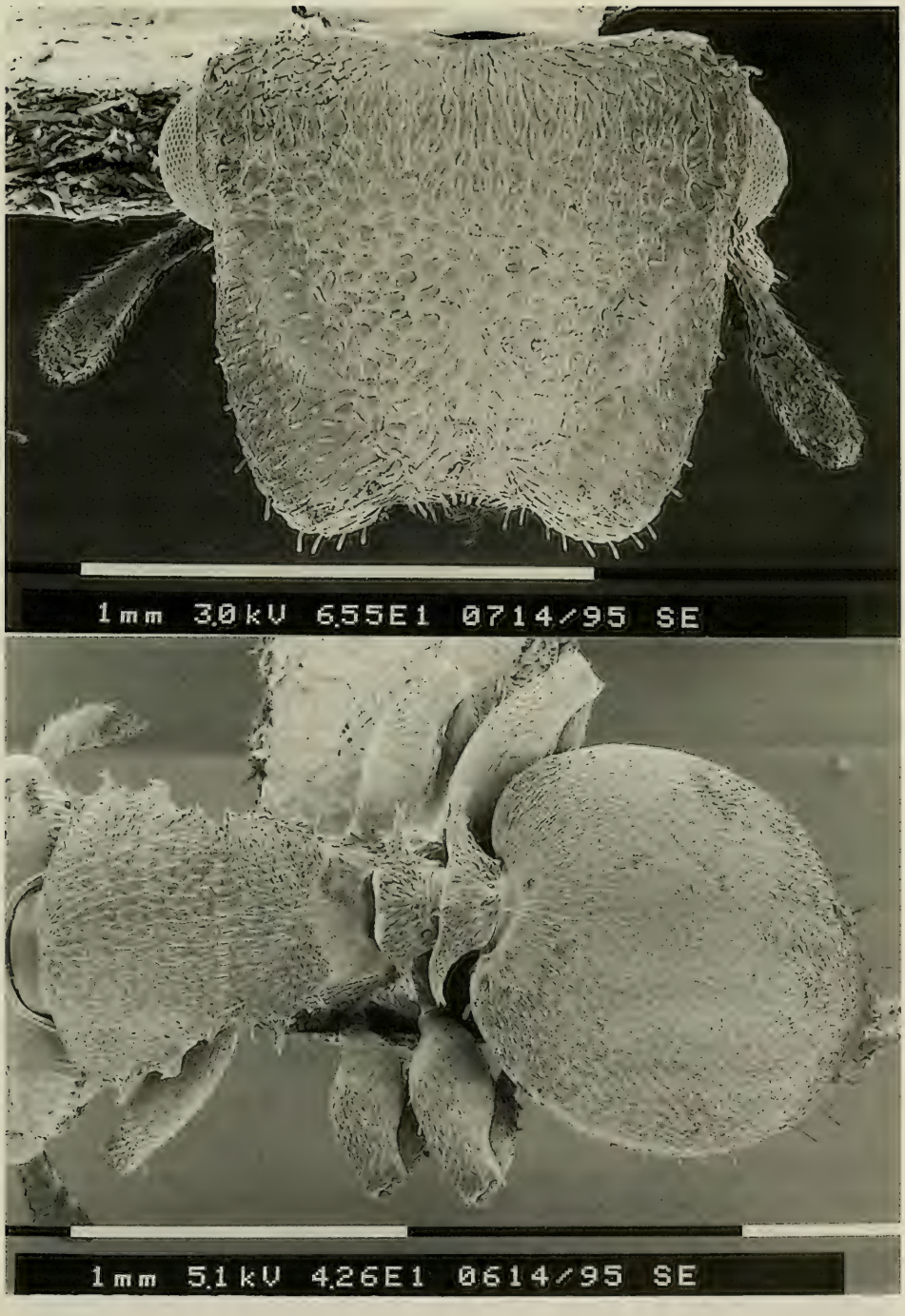


Fig. 286. *Cephalotes chacmul* SNELLING. Worker from Sian Ka'an Sabana (Quintana Roo), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

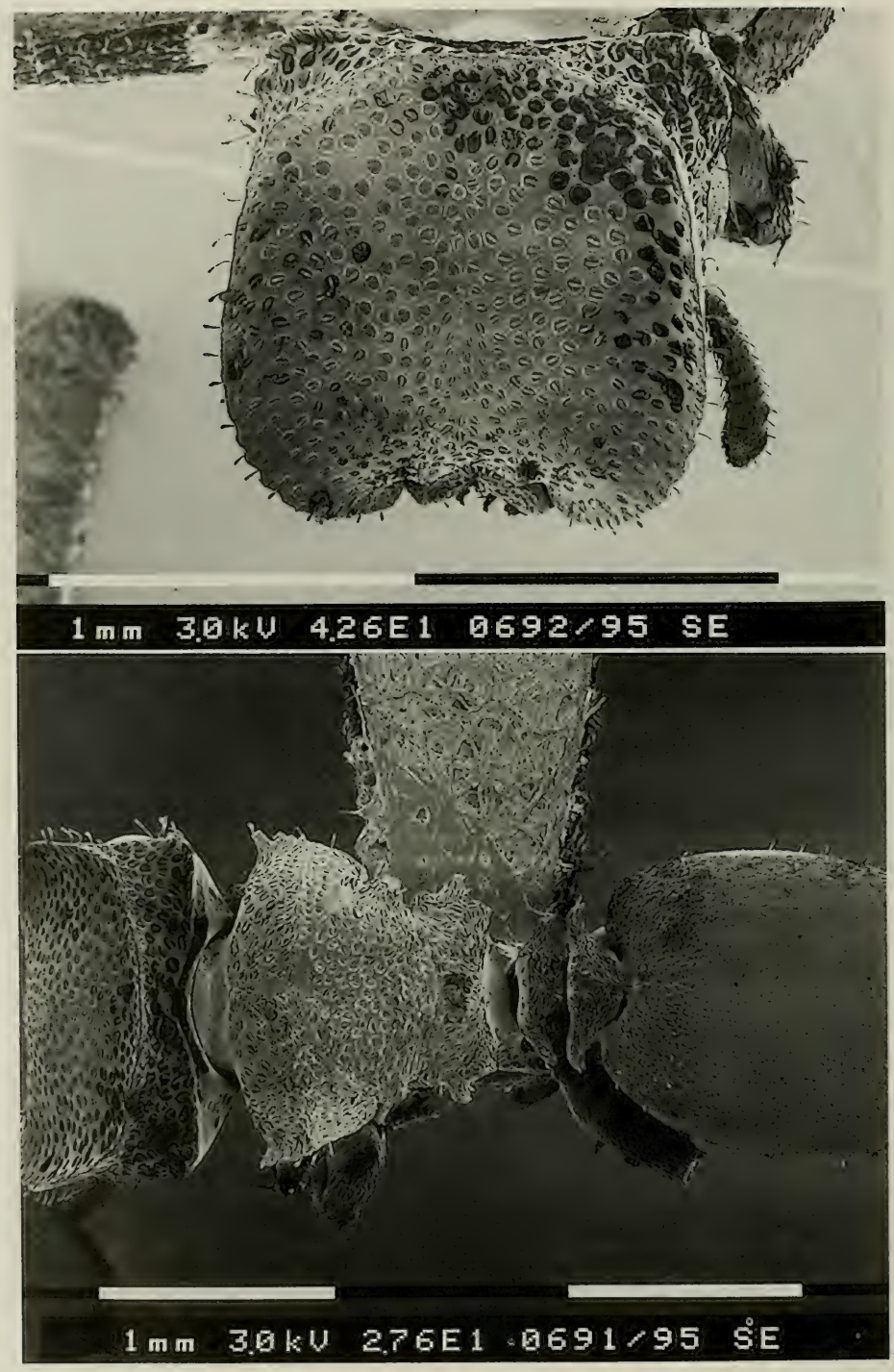


Fig. 287. *Cephalotes chacmul* SNELLING. Soldier from Sian Ka'an, Sabana (Quintana Roo), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

Pronotum, anterior to transverse carina, slightly shiny between irregularly spaced foveae that become crowded laterad; remainder of pronotal dorsum and all of mesoscutum similar but foveae consistently denser; dorsum of propodeum dull, foveae deeper, contiguous and tending to be linearly arranged. All dorsal foveae with glittering scale-like, appressed setae. Side of pronotum with scattered foveae, mostly along posterior one-half, foveae smaller than those of dorsum and many without setae; mesepisternum dull, roughened, with scattered fine foveae and some irregular longitudinal rugulae. Side of propodeum dull, with irregular, widely spaced longitudinal rugulae; posterior face dull, without rugulae.

Procoxa, in lateral view, with large, robust conical process near base. Femora fusiform, without dorsal angulation.

Petiole with vertical anterior face; dorsal face shorter than anterior face, dull and roughened; lateral spines prominent, acute, and slightly curved caudad. Postpetiole strongly convex, dull and roughened, with setose foveae; lateral spines longer and thicker than those of petiole, acute and slightly curved caudad.

Gaster. Base of tergum 1 distinctly invaginated at postpetiolar attachment; distinctly marginate anterolaterally; disc dull and contiguously micropunctate and with sparse, shallow foveae, each with appressed glittering seta; basal one-third with weak, widely spaced longitudinal rugulae. Sternum 1 dull, contiguously micropunctate, and with some weak, longitudinal rugulae, especially at sides.

Dorsum of mesosoma and disc of metasomal tergum 1 with sparse, erect setae about 0.05 mm long; gastral segments also with longer marginal setae.

Color dull blackish; legs more brownish; cephalic shield translucent reddish-brown anterolaterally; gastral tergum 1 with large anterolateral yellowish spots."

Measurements (in mm) and indices: TL 4.98–5.32; HL 1.28–1.40; HW 0.88–1.04; EL 0.28–0.32; PW 1.40–1.44; PeW 0.55–0.61; PpW 0.65–0.72; HBaL 0.32–0.36; HBaW 0.08–0.09; CI 108.6–109.4; PI 100.0–105.5; PPeI 229.5–254.5; PPpI 200.0–215.4; HBaI 22.2–25.0.

Material examined.– **Mexico**: Quintana Roo: Reserva Sian Ka'an, km 11, Sabana, 3–4 June 1986, A. DEJEAN, from pseudobulbs of *Tillandsia balbiciana* (Bromeliaceae), 5 soldiers and 9 workers (holotype and paratypes in LACM, MCZC, and BMNH).

Discussion. - *C. chacmul* is the sister species of *auriger*. The two species are very similar but they can be differentiated by the presence of dense, thick, appressed hairs on the sides and on the center of the posterior part of the first gastral tergite in *auriger* only.

Distribution: Mexico.

Cephalotes auriger DE ANDRADE new species
Fig. 288

Type material: Holotype worker from Mexico, Quintana Roo, S. Miguel, Cozumel Island, VII.1959, N. L. H. KRAUSS; paratype worker same data as the holotype, both in USNM.

Derivatio nominis: From the Latin *auriger* = bearing gold (Cicero), referred to the coloration of the gaster.

Diagnosis. - A member of the *texanus* clade characterised, in the worker, by the thinner and less regular striation on the mesosoma, by the first gastral tergite bearing appressed, dense, broad, golden hairs, and by the presence of a bold area on the posterior border of the first gastral tergite.

Worker (Fig. 288). - Head subquadrate. Frons convex. Frontal carinae superficially crenulate, upturned above the eyes. Vertexal angles round and with crenulate margin. Vertexal margin gently concave medially. Mandibles with superficial lateral carina.

Mesosoma. Scapular angles visible in dorsal view. Anterior pronotal border straight. Pronotal sides with a narrow lamella with three teeth, the first and the second pair pointed, the third obtuse. Promesonotal and propodeal sutures, in dorsal view, impressed on the sides. Mesonotum with a small pair of lateral teeth. Propodeum with differentiate basal and declivous faces; sides of the basal face with two pairs of teeth followed by a pair of denticles, the second pair of teeth larger than the first one; declivous face of the propodeum converging posteriorly.

Petiole. Anterior face truncate, bearing a small pair of denticles dorsally, posterior face sloping posteriorly. Petiolar sides diverging into a pair of long, pointed spines directed backwards, converging posteriorly after the spines. Postpetiolar node gently pointed in the middle dorsally; postpetiolar spines long, pointed, directed slightly forwards at the base and strongly curved backwards at the apex, the sides converging posteriorly after the spines.

Gaster. Oval with a pair of anterolateral, narrow, membranaceous expansions not reaching the stigma posteriorly.

Hind femora angulate. Hind basitarsi long and not broadening at the base.

Sculpture. Head minutely punctate and with foveae broader than their interspaces, diminishing in size anteriorly, denser on the vertexal angles. Frontal carinae with superficial, sparse foveae, sparser anteriorly. Ventral face of the head reticulate, longitudinally rugose, the rugae more irregular on the anterior half where they are superimposed to superficial, oval foveae. Mesosoma minutely reticulate, with superficial, slightly irregular, thin longitudinal, rugosities and foveae, the rugosities more impressed and regular on the propodeum. Pleurae reticulate, with longitudinal, thin, rugosities on the propleurae and dense, superficial, oval foveae on the meso- and metapleurae. Pedicel reticulate and with dense, oval foveae. First gastral tergite minutely reticulate; its anterior third with thin, longitudinal rugae. First gastral sternite minutely punctate and with thin, longitudinal rugosities on the anterior third and on the sides. Middle of the first gastral sternite shining. Legs with the same sculpture as the first gastral tergite but with the foveae more impressed on the distal part of the outer face of femora and tibiae. Posterior face of the femora with longitudinal, thin rugae.

Pilosity. Each fovea with an appressed hair; similar hairs but not originating from the foveae on the whole sides and on the center of the posterior half of the first gastral tergite; remaining parts of the first gastral tergite with thinner and shorter hairs. Sides of the frontal carinae, mesosoma, pedicel and first gastral tergite with slightly clubbed hairs. First gastral sternite and border of the remaining sternites with thin, subdecumbent, sparse, pointed hairs, longer on the border of the first sternite. First sternite also with appressed hairs thicker and shorter than the pointed hairs.

Colour. Black with lighter femora. Mesosomal and pedicellar spines, tibiae and tarsomeres yellowish to light brown, tarsi darker. Frontal carinae yellowish and semi-transparent. First gastral tergite with a pair of oval, anterolateral, orange spots partially hidden by the golden hairs and not surpassing the stigma posteriorly. Gaster, dorsally, and extensor face of the legs covered by thick, golden hairs.

Measurements (in mm) and indices: TL 3.59–4.02; HL 0.86–0.96; HW 0.92–1.04; EL 0.25; PW 0.78–0.89; PeW 0.49; PpW 0.56–0.59; HBaL 0.31–0.33; HBaW 0.07; CI 107.0–108.3; PI 116.8–118.0; PPeI 159.2–181.6; PPpI 139.3–150.8; HBaI 21.2–22.6.

Material examined. - **Mexico**: Quintana Roo: S. Miguel, Is. Cozumel, VII.1959, 2 workers (holotype and paratype), N. L. H. Krauss [USNM].

Discussion. - *C. auriger* is the sister species of *chacmul.* Both species are very similar and - within the *texanus* clade - they share synapomorphically the anterior border of the pronotum separate from the first pair of pronotal teeth and the posterior face of the femora with superficial, longitudinal rugosities. The worker of *C. auriger* can be distinguished from that of *chacmul*, other than by the marked golden pilosity of the gaster, by the rugosities on the dorsum of the mesosoma less impressed, by the first gastral sternite with less longitudinal rugosities, and by the first gastral segment longer. Both species appear to be confined to Central America as it is the case for most species of the *texanus* clade.

Distribution: Mexico.

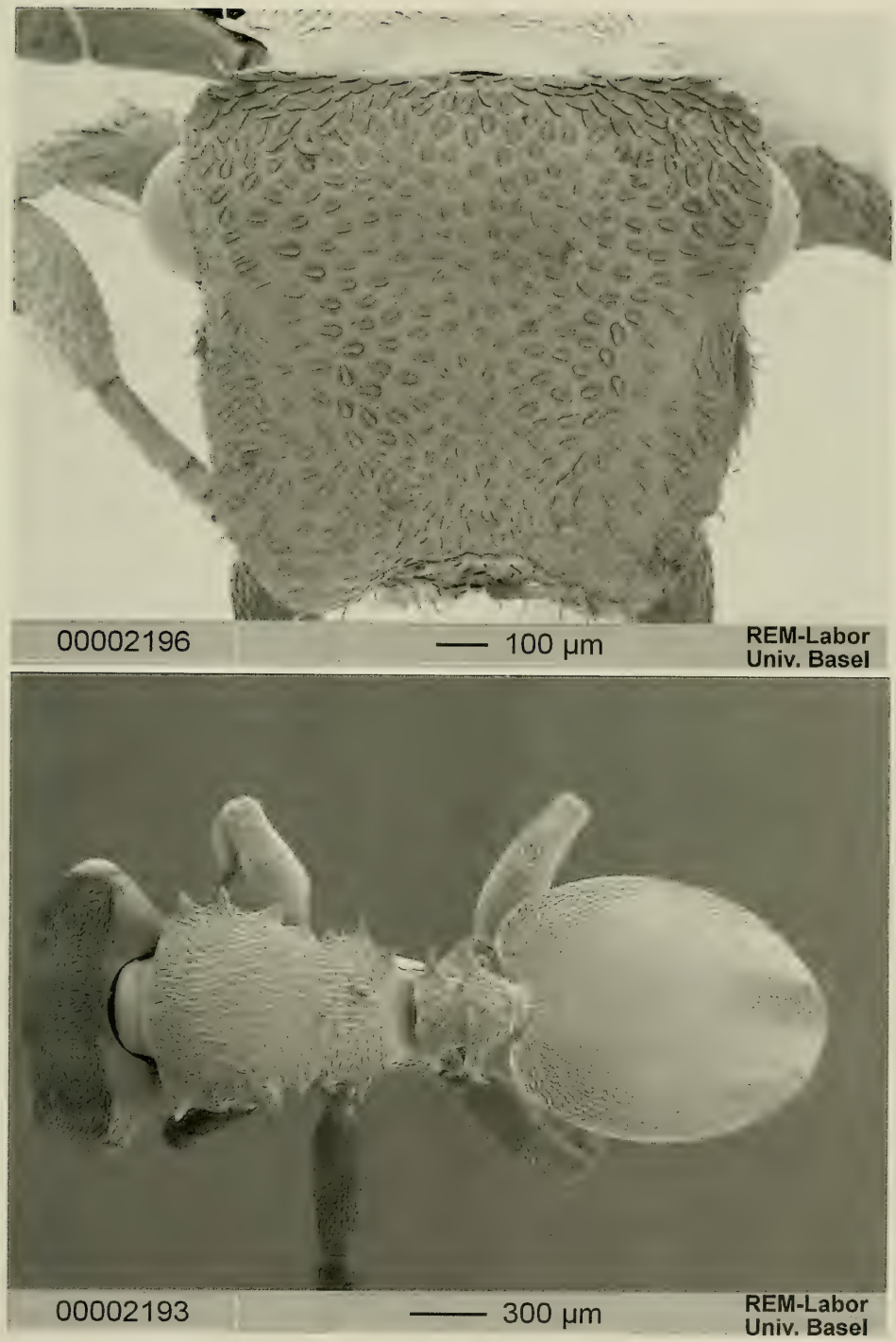


Fig. 288. *Cephalotes auriger* DE ANDRADE. Worker from Cozumel Island (Quintana Roo), Mexico: head (top) and meso- and metasoma (bottom) in dorsal view.

5.6.21. The *bruchi* clade

A clade comprising only one species, *bruchi*, which had been already considered as "remarkably distinctive" by KEMPF (1958 a). In our analysis it is characterised by two synapomorphies: the cephalic disc of the soldier and of the gyne incomplete. The development of the cephalic disc among soldiers and gynes is not parallel in *Cephalotes*. This results clearly from the different distribution of this basically identical character in the two castes. For this reason we felt preferable to code the cephalic morphology of gynes and of soldiers as two separate characters. The resulting independent evolution of the disc among different *Cephalotes* castes may not apply to *bruchi*. In our cladogram, the unknown ancestor of *bruchi* should have had both soldiers and gynes with a complete disc (see Fig. 378). For this species, in fact, the reduction of the cephalic disc appears to be a secondary loss and it is likely to have occurred simultaneously among soldiers and gynes. This isolate case of involution of the disc morphology strengthens the segregate position of *bruchi* in a separate clade.

Negating the secondary loss of the disc in *bruchi* and forcing this species to join the *depressus* clade where the other species with ancestrally incomplete disc are concentrated requires 10 additional evolutionary steps (hypothesis tested by means of only one heuristic search).

Cephalotes bruchi (FOREL) new combination
Figs. 289, 290

Cryptocerus bruchi FOREL, 1912: 202. Worker. Original description. Type locality: Huasan (Catamarca, Argentina). Type material: lectotype worker (implicitly designated by KEMPF, 1958 b) in Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (not available for the present study), 2 workers (syntypes) labelled "Huasan, 1300 m, Argentina, 3.2.1912, C. BRUCH, "in einen Vogelnest 4 Stück", in MHNG, examined.

Cryptocerus ridiculus SANTSCHI, 1915: 207. Soldier. Original description. Type locality: Chaco de Santiago (Argentina). Type material: holotype (unique) labelled "Argentina, Chaco de Santiago del Estero - Río Salado, collection Wagner" in NHMB, examined. Synonymy by KEMPF, 1958 a: 44.

Cryptocerus ridiculus SANTSCHI, BRUCH, 1917: 269. Gyne.

Cryptocerus jheringi pampaensis SANTSCHI, 1931 b: 277. Worker and soldier. Original description. Type locality: Monte Nievas (Argentina). Type material 1 worker, 1 soldier and 1 incomplete soldier labelled "Monte Nievas, Pampa, J. Belsak" in NHMB, examined. Synonymy by KEMPF, 1958 a: 44.

Paracryptocerus bruchi (FOREL), KUSNEZOV, 1953: 338. First combination in *Paracryptocerus*.

Paracryptocerus bruchi (FOREL), KEMPF, 1958 a: 44, figs. 3, 23, 24. Worker, soldier, gyne.

Zacryptocerus bruchi (FOREL), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of a clade of its own which, in addition to the synapomorphies already discussed in the clade description, is easily recognisable by the following combination of characters: in the worker frontal carinae strongly upturned above the eyes and gaster with a pair of solid, broad and protruding lobes; in the soldier and gyne by the incomplete disc, by the postpetiole with broad expansions pointed backwards and by the pronotal carina superficial or absent laterally.

W o r k e r (Fig. 289) (description of KEMPF, 1958 a). - "Total length 5.1–6.0 mm; maximum length of head 1.35–1.61 mm; of thorax 1.61–1.82 mm (lectotype measurements: 5.9,

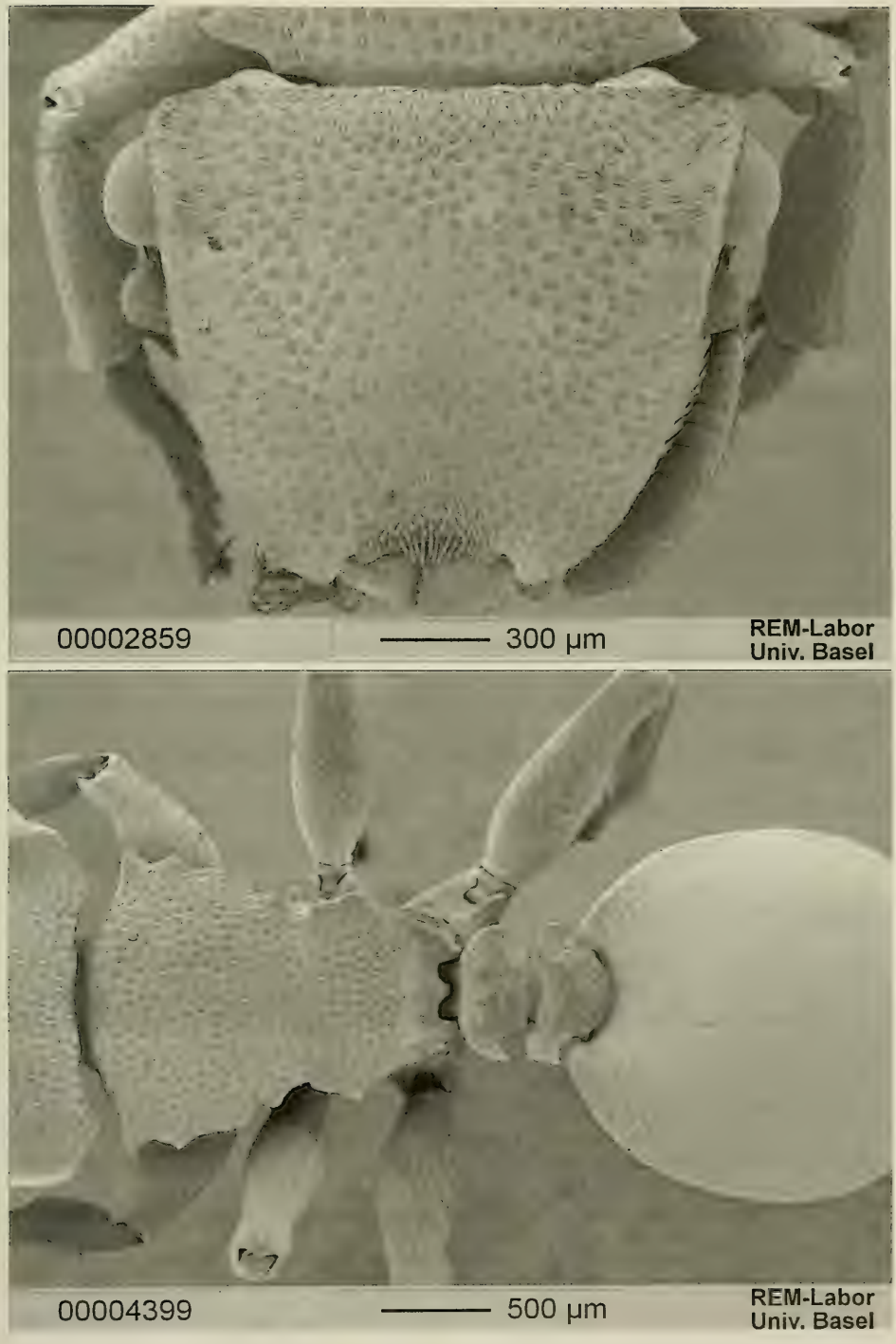


Fig. 289. *Cephalotes bruchi* (FOREL). Worker from Imbirussú-Corumbá (Mato Grosso), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

1.53, 1.82). Measurements of a single worker-soldier intermediate: 6.8, 1.75, 2.02 mm. Black; frontal carinae pale testaceous; tip of scape, and apical tarsites fuscous-ferruginous.

Head subopaque, subquadrate, its maximum length usually scarcely shorter, sometimes longer, than the interocular width. Mandibles rugulose. Frontal carinae semitransparent, their lateral border scarcely crenulate, nearly straight-edged, and conspicuously diverging caudad. Sides of head strongly upturned into a perpendicular position, forming on the inside a longitudinal furrow starting at some distance in front of the eyes and reaching back to the occipital lobes, which are obliquely truncate, with the edge sometimes slightly notched and bearing on the inner corner a strong, opaque, flat, triangular tooth. Eyes bulging, considerably convex, their greatest diameter less than one fourth of the maximum head length. Occipital border concave. Upper face of head gently and evenly convex discad, finely reticulate-punctate, more sparsely covered with squamiferous foveolae. Lower face of head reticulate-rugose discally.

Thorax subopaque. Anterior border gently arcuate. Shoulders subdentate. Sides of pronotum with a tridentate, sharply marginate border, converging caudad. The anteriormost tooth of this border acute and large, the second tooth obtuse, the third subrectangular. Promesonotal suture obsolete. Mesonotum with a blunt, tuberculate tooth on each side. Mesoepinotal suture usually, not always, distinct and slightly impressed. Epinotum sharply marginate on each side, the anterior corner of basal face forming an obtuse tooth followed by a larger, triangular platelike tooth. Declivous face continuous with the basal face, both forming, in profile, an almost even curvature. Dorsum of thorax finely reticulate-punctate, rather densely covered with somewhat elongate squamiferous foveolae. A few very short longitudinal costulae on the anterior border of epinotum in specimens that show a distinct mesoepinotal suture. The lower half of the laterotergite of pronotum longitudinally striate. The greater part of the thoracic pleura more or less longitudinally reticulate-rugose.

Peduncular segments subopaque, the dorso-lateral sculpture as on thorax. Petiole scarcely narrower than postpetiole, its anterior face obliquely truncate, finely reticulate-punctate and slightly shining, lacking all kind of macrosculpture and pilosity. Anterior corners of petiole rounded, continued laterally by a stout, strongly recurved, sharply pointed lateral spine. Postpetiole with slightly concave anterior border, bearing on each side an even more strongly recurved and pointed spine, resembling a pigeon wing. Upper face of postpetiole convex, often vestigially acuminate discally.

Gaster short, oval, rather shining, its median length usually scarcely exceeding the maximum width, deeply excised antero-mesally, between the submarginate, strongly projecting anterolateral gastral lobes. First tergite finely reticulate-punctate, with sparse piligerous punctures.

Standing hair confined to the apex and venter of gaster. Scalelike hair of head and thorax and peduncle canaliculate and appressed; of gaster simple, thin, but appressed."

Measurements (in mm) and indices: TL 5.76–6.28; HL 1.32–1.46; HW 1.46–1.68; EL 0.34–0.36; PW 1.16–1.42; PeW 0.60–0.66; PpW 0.64–0.70; HBaL 0.60–0.72; HBaW 0.17–0.20; CI 110.6–123.5; PI 118.3–125.8; PPeI 206.0–243.3; PPpI 202.8–228.1; HBaI 27.8–28.6.

S o l d i e r (Fig. 290) (description of KEMPF, 1958 a). - "Total length 8.4–10.6 mm; maximum length of head 2.39–3.10 mm; of thorax 2.50–2.96 mm. Black; anterolateral corners of head to a variable extent fuscous yellowish-red; tip of scape, apical funicular segments, extensor face of tibiae and apical tarsites fuscous-ferrugineous.

Head shining, subquadrate, little or scarcely broader than long, without a distinct, completely marginate disc above. Anterolateral borders vestigially crenulate, posterior border sharply marginate above the truncate occiput, postero-lateral border of upper face immarginate, i. e. the disc surface is continuous with the occipital lobes. Dorsum of head scarcely convex, almost flat, slightly excavated anterolaterally above the antennal scrobes. Clypeal sutures and midfrontal suture well marked, the latter extending beyond the middle of head. Occipital lobes terminating in a stout, solid tooth. Eyes little convex. Lower border of cheeks carinate. Upper face of head and sides finely punctate, with sparse squamiferous, rounded foveolae, separated from each other by a distance which exceeds their own diameter. Lower face of head foveolate. Cheeks and mandibles reticulate-rugose and foveolate.

Thorax less shining than head. Pronotum nearly as broad as head, its anterior angle with a stout tooth, which is blunt at apex. Sides of pronotum gently sinuous, gently converging caudad, the posterior corner rounded. Transverse pronotal carina bisinuate, bluntly edged, interrupted in the middle. Promesonotal suture vestigial. Lateral lobes of mesonotum obliquely truncate, immarginate. Mesoepinotal suture distinct and impressed. Basal face of epinotum with a little projecting, broad, rounded lobe on each side, and a stronger, apically rounded tooth on the posterior corner, projecting upward and obliquely laterad. Declivous face about twice as long as basal face, slightly excavated discally, immarginate at the sides. Sculpture of dorsum of thorax as on upper face of head, the microsculpture being a bit stronger, and the foveolae more crowded. Sides of thorax with more elongate foveolae, and a reticulate-rugose area on the posterior half. Middle and hind basitarsi slightly broadened and flattened at base.

Peduncular segments subopaque, the dorso-lateral sculpture as on dorsum of thorax. Postpetiole distinctly broader than petiole. Lateral spines of both segments equally recurved, their apices not very acute.

Gaster rather short, oval, subopaque, its greatest width at the middle of its length. Shallowly emarginate antero-mesally, the anterolateral lobes much less projecting than in worker. First tergite finely, but sharply and densely punctate, with sparse, piligerous punctures.

Scalelike hair in the foveolae, as a rule, short and inconspicuous, especially on head, more visible and longer on pronotum and sides of thorax. Very small and simple on first gastral tergite. Standing hair, as usual, in this caste, confined to the tip and venter of gaster."

Measurements (in mm) and indices: TL 9.66–10.56; HL 2.30–2.60; HW 2.60–3.08; EL 0.42–0.48; PW 2.44–2.84; PeW 0.92–1.08; PpW 1.02–1.16; HBaL 0.70–0.72; HBaW 0.21–0.24; CI 113.0–118.5; PI 106.5–108.4; PPeI 262.9–265.2; PPpI 239.2–244.8; HBaI 30.0–33.3.

G y n e (translation of the description of BRUCH, 1917). - "Long, 11 millimetres. With the same colour as the soldier, i. e. black, the anterior part of the head, the antennae and the legs brown-reddish.

Moderately shining; the abdomen is more opaque, due to the presence on its surface of a reticulate punctuation, more pronounced than over the head and the thorax. The latter are covered by large points or small pits slightly larger over the head and which are at the same time larger than in the soldier, but smaller and less deep on the abdomen. Each pit carries a flattened hair, short and decumbent, much thinner on the abdomen, which has also a few setae on its extremity.

The head is square, as in the soldier, slightly smaller (2.5 x 2.5 mm); its sides are also parallel, the posterior angles straight, the borders slightly sinuous and not crenulate; it exists also a weak spine in the lower third of the posterior border. The ocelli, arranged in a regular triangle, are slightly larger than the size of the small pits.

The thorax is half longer than broad (3.1 x 2.2 mm); all narrower than the one of the soldier. The lateral teeth of the epinotum are narrower. The two peduncular nodes are slightly longer, the first is weakly toothed laterally; the second, i. e. the postpetiole as in the soldier. The abdomen is twice longer than broad, cylindrical and also strongly notched at the base.

Width of the pronotum 2.2 mm, of the epinotum 1.2 mm, of the abdomen 2.2 mm; length of the thorax 3.2 mm, of the abdomen 5 mm."

Measurements (in mm) and indices: TL 12.20–12.62; HL 2.24–2.28; HW 2.48–2.56; EL 0.45–0.48; PW 2.28–2.52; PeW 0.88–0.92; PpW 1.08–1.16; HBaL 0.83–0.88; HBaW 0.24–0.25; CI 110.7–112.3; PI 101.6–108.8; PPeI 259.1–273.9; PPpI 211.1–217.2; HBaI 28.4–28.9.

M a t e r i a l e x a m i n e d . - **Brazil**: M a t o G r o s s o d o S u l : Imbirussú-Corumbá, 1.XII.1960, 5 workers, K. LENKO [MZSP].

Argentina: C a t a m a r c a : no further locality, 1 worker, A. GOMEZ [MZSP]; Huasán, 3.II.1912, 1300 m, 2 workers (syntypes), C. BRUCH [MHNG]; Icaño, Mistol Paso, 1 soldier, 1 gyne, E. R. WAGNER [NHMB]. T u c u m á n : Tapia, 1 worker, N. KUSNEZOV [MZSP]. S a n t i a g o d e l E s t e r o : no further locality, 1 soldier [MZSP]; Río Salado, 1 soldier (type of *ridiculus*), E. R. WAGNER [NHMB]; Chaco de Añatuya (Tintina), 1 soldier, E. R.

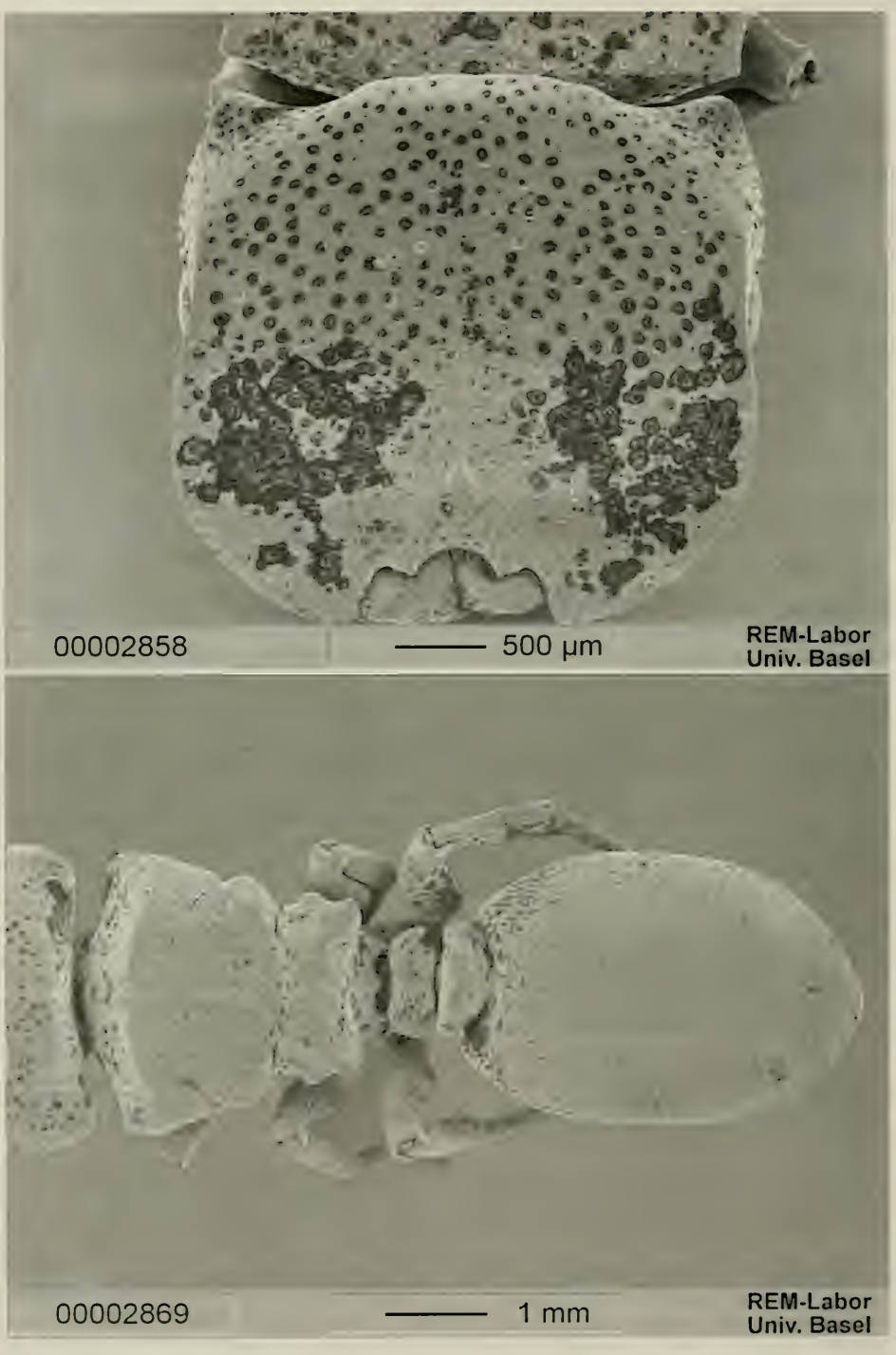


Fig. 290. *Cephalotes bruchi* (FOREL). Soldier from Chaco de Anatuya Tentina, Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

WAGNER [NHMB]; Girardet, 1 worker [MZSP]. S a n t a F é : Rosario, 1 soldier, W. M. DAVIS [MCZC]. L a P a m p a : Monte Nievas, 1 worker, 1 incomplete soldier, 1 soldier (syntypes of *jheringi pampaensis*) J. BELSAK [NHMB].

D i s c u s s i o n . - The specimens from Mato Grosso differ from the type series in having the body more opaque and with much more impressed reticulation, by the petiolar dorsum with a pair of small denticles and by the gastral lobes, shorter.

D i s t r i b u t i o n : Argentina and Brazil (Mato Grosso).

5.6.22. The *fiebrigi* clade

A relatively large clade comprising 10 species confined to the southernmost portion of the distribution of *Cephalotes* and extending up to Mato Grosso to the North. The worker propodeum with three or four lateral denticles results synapomorphic for the clade, although both morphologies can be homoplastically present also among members of other species groups. The sole known four males of the clade, moreover, share also very long gonostyli. All these characters separate the members of the clade from their closest relatives with which they share the solid membranaceous border of the gastral expansions.

Species included in the clade: *bohlsi*, *fiebrigi*, *fossithorax*, *guayaki*, *jheringi*, *lanuginosus*, *liogaster*, *pilosus*, *quadratus*, *supercilii*.

Cephalotes bohlsi (EMERY) new combination
Fig. 291

Cryptocerus bohlsi EMERY, 1896: 631, fig. C. Worker and soldier. Original description. Type locality: San Salvador (Paraguay). Type material 1 worker and 2 soldiers in MCSN, 1 worker 1 soldier in MHNG all syntypes and labelled only Paraguay, examined.

?*Cryptocerus bohlsi* var. *medusa* SANTSCHI, 1919: 45. Soldier. Original description. Type locality: Mato Grosso (Brazil). Type material possibly lost: the specimen labelled as "Type" in NHMB is from Argentina (Gran Chaco) and not from Brazil. Synonymy by KEMPF, 1958 a: 101.

Paracryptocerus bohlsi (EMERY), KEMPF, 1958 a: 101. First combination in *Paracryptocerus*.

Zacryptocerus bohlsi (EMERY), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *fiebrigi* clade differing from its closest species, *jheringi*, in the worker and in the soldier by the sculpture less impressed and by the foveae sparser.

W o r k e r (Fig. 291). - Head subquadrate. Vertexal angles round, with a narrow, semitransparent lamellaceous border, continuos or with a small, obtuse tooth. Vertexal margin concave. Frontal carinae weakly upturned over the eyes. Mandibles laterally carinate.

Mesosoma gently convex in side view. Scapular angles visible in dorsal view. Pronotal sides with a narrow lamella with three pairs of teeth, the first pair more pointed. Sides of mesonotum with a pair of small teeth. Promesonotal suture superficially impressed. Propodeal suture impressed laterally and interrupted medially. Propodeum with differentiate basal and declivous faces and with the sides narrowing backwards; sides of the basal face of the propodeum with two pairs of teeth, the first pair sometimes simply angulate and the second one larger; sides of the declivous face of the propodeum posteriorly with a narrow, semitransparent lamella unarmed or with one or two pairs of denticles.

Petiole anteriorly truncate; its anterior border superficially concave medially. Petiolar spines arising from the anterior face of the petiole, pointed and curved backwards. Postpetiole

as broad as or slightly broader than the petiole, with broad lateral expansions, strongly developed anteriorly, curved and pointed backwards.

Gaster suboval, with a pair of broad anterolateral lobes with a marked margin not surpassing the stigma posteriorly.

Mid and hind femora not angulate; mid and hind basitarsi flat and with subparallel sides.

Sculpture. Head dorsum and mesosoma minutely reticulate, the reticulation more impressed on the mesosoma, and with small, superficial foveae, deeper, denser and larger on the posterior fourth of the head and on the anterior part of the pronotum, shallower on the frontal carinae. Ventral face of the head minutely reticulate and with dense, suboval foveae and irregular, longitudinal rugosities less impressed in the middle. Pleurae reticulate, with few, thin, longitudinal rugosities on the propleurae and with oval foveae on the lower meso- and metapleurae. Pedicel with the same sculpture as the mesosoma but more irregular.

First gastral tergite minutely reticulate, with small, very superficial foveae and with few, thin, longitudinal rugosities close to the postpetiolar articulation. First gastral sternite with reticulation larger than the one on the corresponding tergite, less impressed in the middle of its posterior half.

Legs reticulate and with superimposed small, oval foveae on the outer face of the femora and tibiae.

Pilosity. Body with three types of hairs: (1) appressed and generally originating from each fovea, of size proportional to the one of the fovea from which they originate, i. e. larger on the posterior fourth of the head dorsum and on the anterior part of the pronotum; much shorter and thinner on the body parts without foveae; (2) slightly clubbed, rare, on the sides of the frontal carinae and on the legs; slightly longer on the posterior borders of the gastral segments; (3) long and pointed on the posterior border of the gastral sternites.

Colour. Black. Frontal carinae, mesosomal and peduncular spines yellowish to light brown. Outer face of the mid and/or fore tibiae brown.

Measurements (in mm) and indices: TL 4.54–4.96; HL 1.06–1.16; HW 1.18–1.32; EL 0.28–0.34; PW 1.02–1.20; PeW 0.54–0.57; PpW 0.55–0.56; HBaL 0.37–0.43; HBaW 0.13–0.14; CI 111.3–113.8; PI 110.0–115.7; PPeI 178.9–222.2; PPpI 185.4–214.3; HBaI 30.2–37.8.

S o l d i e r . - Head almost as broad as long, with complete disc. Floor of the disc gently convex posteriorly and oblique anteriorly. Borders of the disc not raised. Sides of the disc narrowing backwards, not hiding the eyes and connected by a truncate or subconvex border thicker than the one on the sides. Frontal carinae weakly crenulate. Vertexal angles broad and obtuse. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a longitudinal, denticulate carina just in front of the eyes.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of small teeth. Pronotal sides straight. Pronotal crest marked, thickening from the sides towards the center where it is interrupted by a sulcus. Promesonotal suture impressed. Sides of the mesonotum with a broad, round tooth. Propodeal suture deeply impressed. Propodeum with well differentiate basal and declivous faces. Sides of the basal face with a small protuberance followed by a pair of short, broad, triangular teeth and by a pair of large, stout teeth curved upwards. Declivous face concave in the middle; its sides converging, carinate laterally and with or without a minute pair of denticles posteriorly.

Petiole with the anterior face truncate and superficially concave medially; its sides with a pair of short, pointed spines curved backwards. Postpetiole convex. Postpetiolar sides with a pair of thick, round expansions arising from the anterior border and directed anterolaterally.

Gaster oval and with a pair of protruding, anterolateral lobes.

Mid and hind femora without angle or denticle. Hind basitarsi slightly more compressed apically than distally and with subparallel sides.

Sculpture. Head dorsum moderately shining, punctate and with superficial, variably clumped, small foveae shallower on the frontal carinae, the punctuation more impressed on the posterior half. Ventral part of the head shining, sparsely punctate-foveolate. Mesosoma reticulate-punctate and with dense, small foveae, larger on the pronotum, sparser on the basal

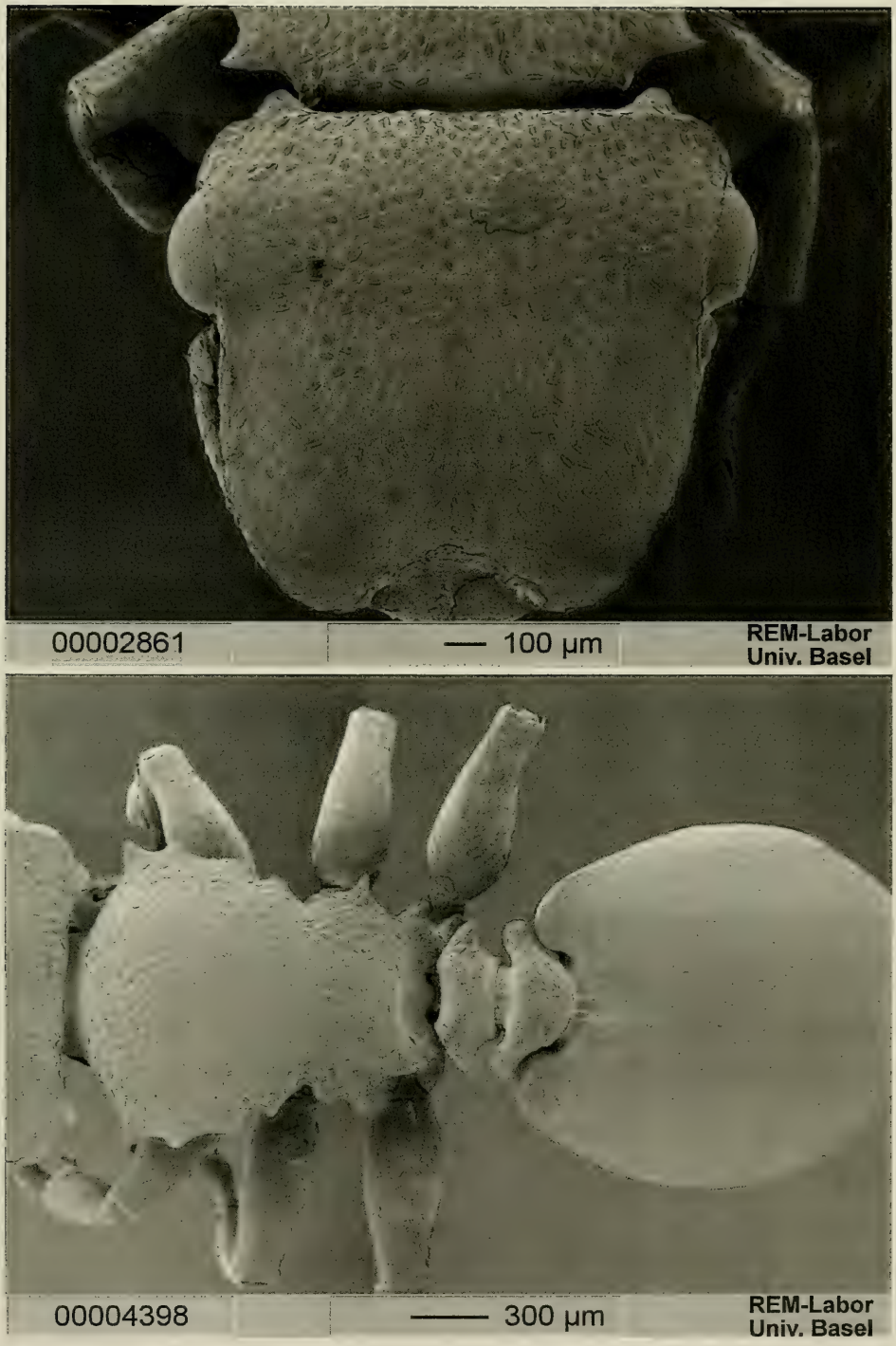


Fig. 291. *Cephalotes bohlsi* (EMERY). Worker from Argentina (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

face of the propodeum and absent on the declivous one. Pleurae reticulate, with sparse, suboval foveae, denser on the lower mesopleurae. First gastral tergite reticulate and with superficial, oval foveae slightly more impressed on the anterior third. Remaining tergites and sternites reticulate, the reticulation more superficial on the posterior half of the first gastral sternite and on the remaining sternites. Legs simply reticulate. Outer face of the femora and of the tibiae with superficial, oval foveae.

Pilosity. As in the worker.

Colour. Sides and ventral part of the head, mesosoma, pedicel and gaster black; legs lighter with the outer face of the tibiae brown. Frontal carinae and border of the disc dark orange to light brown. Remaining head dorsum dark brown.

Measurements (in mm) and indices: TL 7.56; HL 1.84; HW 1.80; EL 0.36; PW 1.68; PeW 0.73; PpW 0.75; HBaL 0.46; HBaW 0.16; CI 97.8; PI 107.1; PPeI 230.1; PPpI 224.0; HBaI 34.8.

Material examined. - **Paraguay**: no further locality on the label under the specimens (should be San Salvador in the department of Concepción), 2 workers (syntypes), 3 soldiers (syntypes), BOHLS [MCSN, MHNG].

Argentina: Gran Chaco, 1 soldier (putative holotype of v. *medusa*) [NHMB]. Formosa: Las Lomitas, XI.1950, 1 worker, DAGUERRE [USNM]; same locality, 23.V.1951, 1 worker [MZSP]; Laishi, 1 worker [NHMB].

Discussion. - *C. bohlsi* appears to be a rare species. The workers are quite similar to those of *jheringi* but the soldiers allow an easy separation of the two species. Besides of the character already mentioned in the diagnosis, another character useful to separate workers and soldiers of both species is the shape of the expansions of the peduncular segments, much larger and broader in *bohlsi* than in *jheringi*. The soldiers of *bohlsi* and *jheringi* are easily distinguishable for the foveae of the body much smaller, sparser and more superficial in *bohlsi* than in *jheringi*.

The head of the soldier of *bohlsi* resembles somehow the one of *bruchi* in sculpture and shape of the disc, but in *bohlsi* the posterior border of the sides of the disc is more marked than in *bruchi*.

The unique soldier of the var. *medusa* in the NHMB is labelled as type by SANTSCHI and corresponds to the description of SANTSCHI (1919) but it is from Gran Chaco (Argentina) and not from Mato Grosso (Brazil) from where the variety had been originally described. The var. *medusa*, however, had been described from Mato Grosso (the Brazilian prolongation of the Argentinean Gran Chaco) in a paper on the "Formicides de la République Argentine". This soldier differs from the sole three soldiers of *bohlsi* known so far for the body punctuation more impressed, deeper and denser, for the larger foveae and for the colour, darker. We prefer to still consider the variety *medusa* a synonym of *bohlsi* as suggested by KEMPF (1958 a) in an intuitive way (he did not examine the sole specimen referable to this name) until the collection of additional material will allow a decision on a firmer basis.

Distribution: ? Brazil (Mato Grosso), Argentina, Paraguay.

Cephalotes jheringi (EMERY) new combination
Figs. 292, 293, 294, 295, 296

Cryptocerus jheringi EMERY, 1894 a: 205, figs. 13, 14. Worker and soldier. Original description. Type locality: Rio Grande do Sul (Brazil). Type material: 2 syntype workers labelled „Rio Grande, Ihering", in MCSN, examined. Note: A syntype of *jheringi* presumably part of the material originally examined by EMERY and preserved in the MHNG is actually *pallidicephalus*.

Cryptocerus peltatus EMERY, 1896: 633, fig. D. Soldier, gyne. Original description. Type locality: San Salvador (Paraguay). Type material: 1 soldier (without gaster) and 1 gyne, syntypes, labelled "Paraguay, Bohls", in MCSN, examined. Synonymy by KEMPF, 1958 a: 50.

Cryptocerus peltatus Ellenriederi FOREL, 1911: 258. Worker, soldier, gyne. Original description. Type locality: Rosario de Santa Fé (Argentina). Type material: 1 worker, 1 soldier (syntypes) in MHNG, 2 workers, 1 soldier, 1 gyne (syntypes), in ZSMC, all labelled "*Cr. peltatus* Em, r. *Ellenriederi*, type, Forel, Rosario de Santa Fé, in Weidenstamm", examined. Synonymy by KEMPF, 1958 a: 50.

Cryptocerus peltatus Ellenriederi FOREL, BRUCH, 1916: 321, partim, ?fig. 13 (could be also *bivestitus*), non pl. 9, fig. 14 (= *bivestitus*). Worker. Misidentification proposed by KEMPF (1958 a: 50) and confirmed by our examination of part of the relevant material.

Paracryptocerus jheringi (EMERY), KUSNEZOV, 1953: 338. First combination in *Paracryptocerus*.

Paracryptocerus jheringi (EMERY), KEMPF, 1958 a: 50, figs. 5, 12, 14, pl. 2, fig. 2, pl. 3, fig. 6. Worker, soldier and gyne.

Zacryptocerus jheringi (EMERY), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Zacryptocerus iheringi [sic] (EMERY), VIERBERGEN & SCHEVEN, 1995: 168, fig. 12. Worker.

D i a g n o s i s . - A member of the *fiebrigi* clade differing from its next outgroup species, *bohlsi*, in the worker and in the soldier by the sculpture more impressed and by the denser foveae, and, from the next ingroup species, *fossithorax*, in the worker, soldier and gyne by the mesosoma and pedicel without short, truncate hairs.

W o r k e r (Fig. 292). - Head almost as long as broad in small specimens and broader than long in large ones. Vertexal angles round or subtruncate and marginate; a very narrow lamellaceous border present in few specimens only. Vertexal margin concave. Frontal carinae not upturned over the eyes. Mandibles laterally carinate.

Mesosoma gently convex in side view. Scapular angles visible in dorsal view. Pronotum with a narrow lateral lamella with three pairs of irregular teeth, sometimes the first pair more pointed and the second and third pairs simply angulate. Sides of mesonotum with a pair of small teeth. Promesonotal suture superficially impressed. Propodeal suture more impressed laterally than medially. Propodeum with differentiate basal and declivous faces and with the sides narrowing backwards; sides of the basal face of the propodeum with two pairs of teeth, the first pair sometimes simply angulate and the second one larger; sides of the declivous face of the propodeum unarmed or armed with one or two pairs of denticles.

Petiole anteriorly truncate; its anterior border superficially concave medially. Petiolar spines arising from the anterior face of the petiole or slightly behind it, pointed and curved backwards. Postpetiole broader than the petiole; its lateral expansions variable in width, developed anteriorly, curved and pointed backwards.

Gaster suboval, with a pair of broad, anterolateral lobes with a thick, dark, marked margin not surpassing the stigma posteriorly; sometimes the lobes less thick and semitransparent.

Mid and hind femora not angulate; mid and hind basitarsi flat and with subparallel sides.

Sculpture. As in *bohlsi* except for the reticulation more impressed and for the foveae denser and larger.

Pilosity. As in *bohlsi* except the distribution of the hairs of type (2) which is denser on the sides of the frontal carinae and on the posterior borders of the gastral segments and the one of the hairs of type (3), rare to sparse on the whole first sternite.

Colour. Black. Frontal carinae, mesosomal and peduncular spines and border of the gastral lobes yellowish to light brown. Outer face of the tibiae brown.

Measurements (in mm) and indices: TL 3.36–5.36; HL 1.08–1.24; HW 1.10–1.44; EL 0.33–0.35; PW 0.99–1.24; PeW 0.50–0.61; PpW 0.63–0.69; HBaL 0.37–0.49; HBaW 0.10–0.13; CI 101.8–116.1; PI 111.1–116.1; PPeI 198.0–203.3; PPpI 157.1–179.7; HBaI 26.5–27.0.

S o l d i e r (Fig. 293) (description of KEMPF, 1958 a). - "Total length 5.5–7.9 mm (specimens under 6.0 mm are generally intermediates between this and the worker caste);

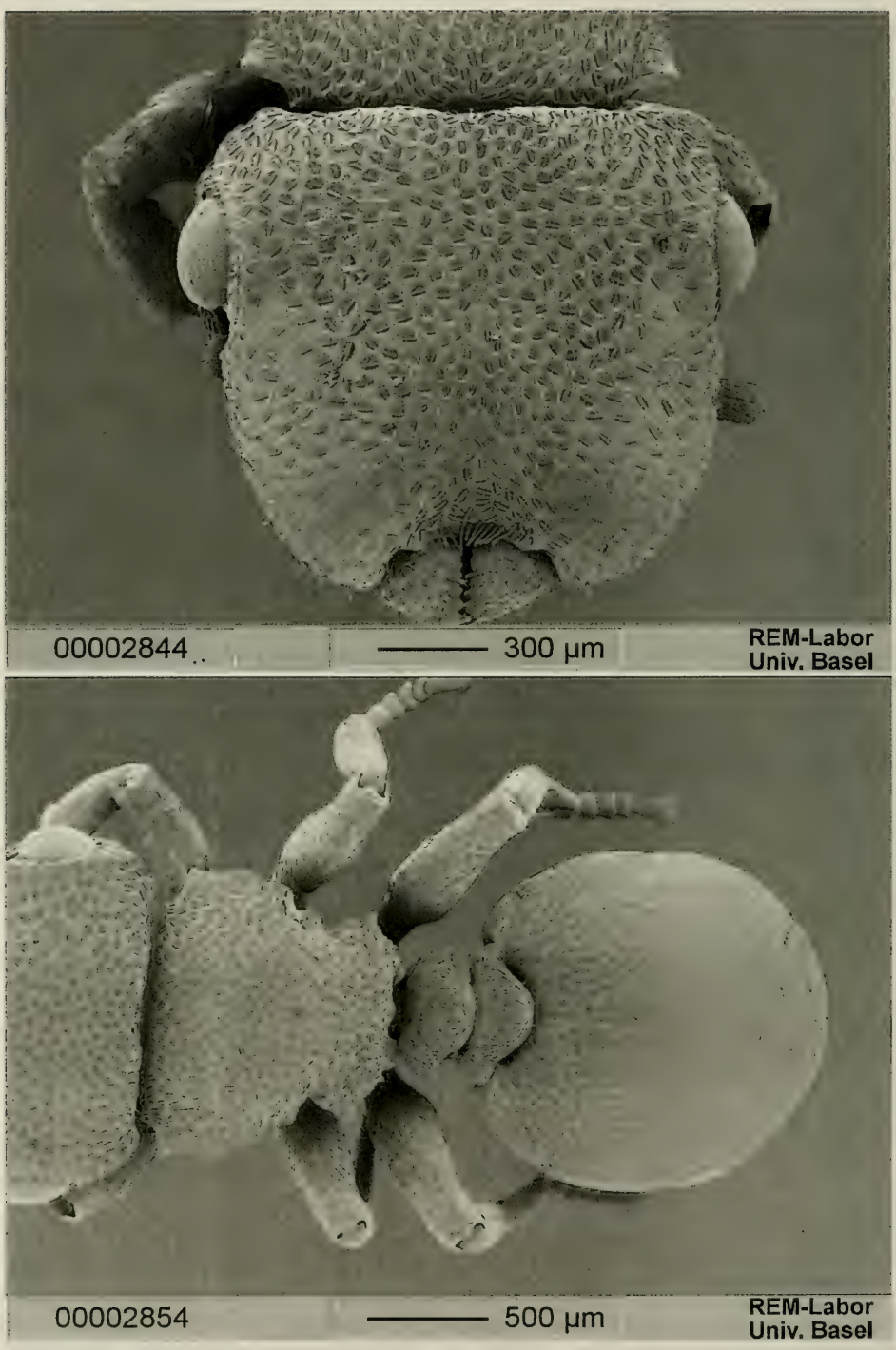


Fig. 292. *Cephalotes jheringi* (EMERY). Worker from San Fernando, Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

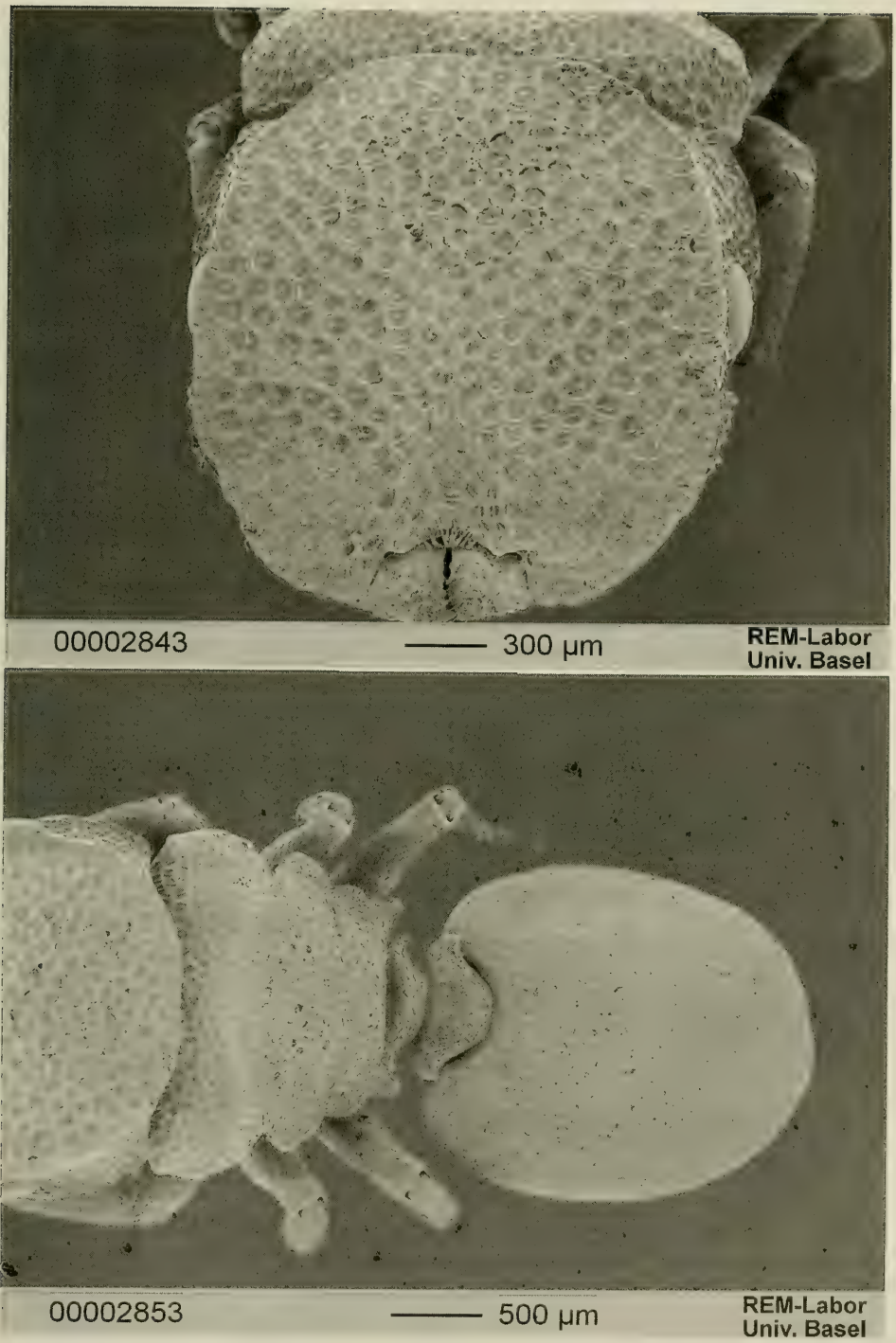


Fig. 293. *Cephalotes jheringi* (EMERY). Soldier from San Fernando, Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

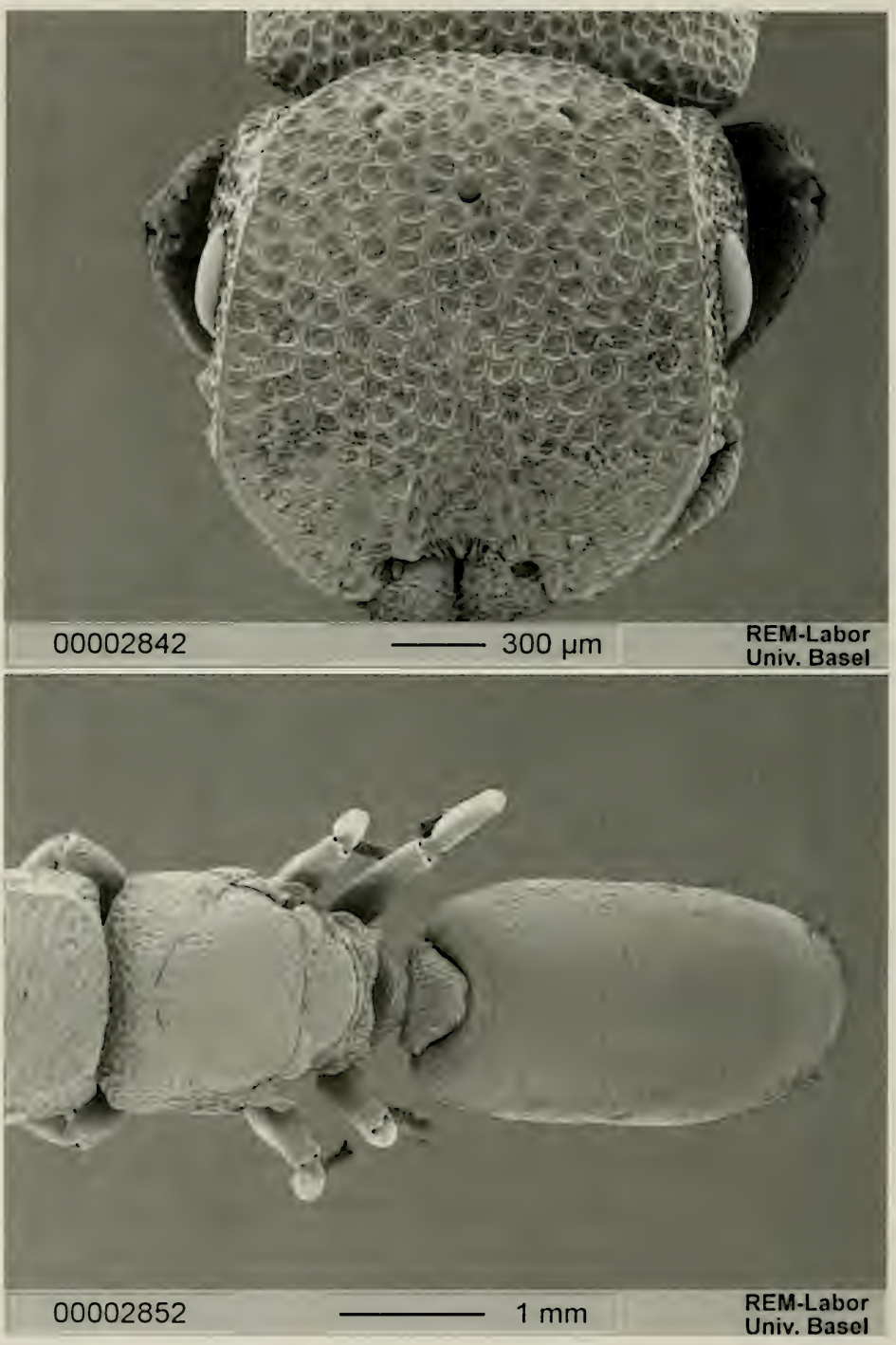


Fig. 294. *Cephalotes jheringi* (EMERY). Gyne from San Fernando, Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

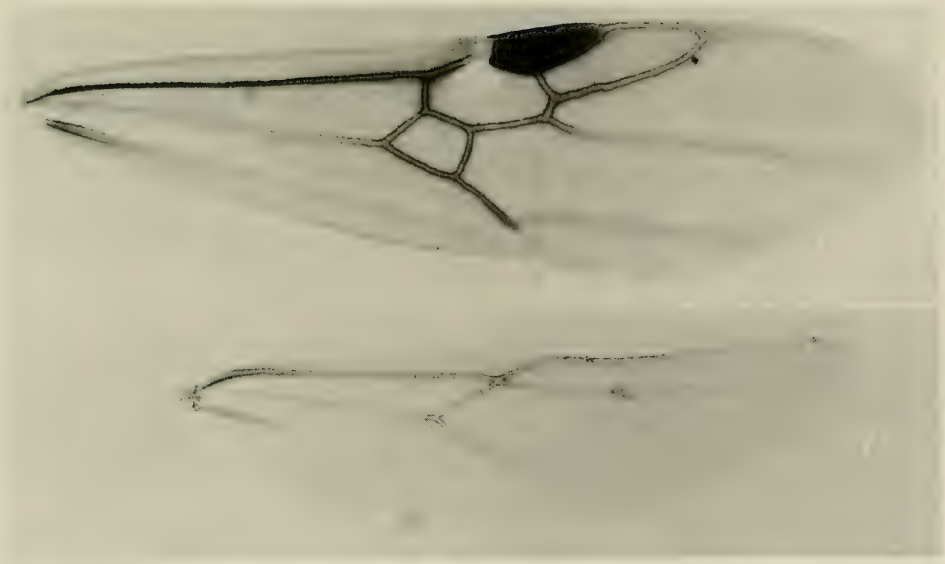


Fig. 295. *Cephalotes jheringi* (EMERY). Gyne from San Fernando, Argentina, fore and hind wings.

maximum length of head disc 1.61–2.25 mm; of thorax 1.61–2.14 mm. Maximum width of head disc 1.50–2.07 mm. Black; yellowish-brown to testaceous: anterolateral portions of head disc, or nearly the entire head disc, both dorsally and the sides (in this case, there is usually a median black spot on the center of the disc, near the vertex of the clypeal triangle), anterolateral portions of pronotum, extensor face of tibiae; ferruginous: tip of mandibles and scapes, first funicular segment, the four apical tarsites. In darker specimens the yellow color may be substituted by ferruginous, and the ferruginous color by fuscous-ferruginous. A single soldier from Tafi Viejo, Tucumán, of an otherwise completely black series, has a uadrimaculate gaster.

Head disc subquadrate to subrectangular, completely marginate round its scarcely raised, somewhat crenulate border; the anterior corner rounded, the posterior corners either obliquely truncate or rounded. Floor of disc rather flat, slightly excavated anterolaterally. In profile, the sides of the head do not cover the dorsum of the cephalic disc, and the distance between the upper border of the eye and the rim of the disc is much less than the diameter of the eye. Sides of disc subparallel. Occipital border straight in smaller specimens, rounded in larger specimens. Occipital borders either bluntly rounded, or angulate or even subdentate. Floor of disc, sides of head, and occiput reticulate-punctate and foveolate in smaller specimens, whereas in larger specimens the foveolae are close together and the intervals form a network of raised rugosities. Lower face of head reticulate-punctate with sparse, elongate foveolae, and a few rugosities anterolaterally.

Thorax subopaque. Shoulders dentate. Sides of pronotum at the level of the usually vestigial, never strongly marked nor crested transverse carina, forming a blunt angle, the posterior corner of the pronotum being subrectangular. Mesonotum with a subtruncate projecting lateral lobe. Mesoepinotal suture distinct, scarcely impressed mesally. Sides of basal face of epinotum usually with two lateral, angulate or rounded and slightly projecting lobes and a stouter tooth at the posterior corner. Declivous face slightly excavated, its sides marginate. Mesopleural tooth absent. Sculpture, in general, as on head, but the foveolae are smaller, the intervals often shining. Laterotergite of pronotum longitudinally costate at the lower half. Pleura more or less rugose.

Peduncular segments usually equal in width (not always, sometimes the postpetiole is distinctly broader!). Postpetiole greatly convex middorsally. Gaster elongate-ovate. Anterolate-

ral lobes solid, submarginate, not crested. First tergite finely reticulate-punctate, the anterior fifth having fine longitudinal rugosities. Piligerous punctures scarcely impressed, inconspicuous.

Pilosity, in general, not differing from that of *bivestitus*, and *fossithorax*, with the exception of the following: Foveolae of head disc with short, thick, more or less decumbent hair, the free end of which does usually not project beyond the rim of the pit. Rim of cephalic disc with sparse, thick, subclavate, projecting setae. Scalelike hair of thorax, peduncle, and gaster appressed."

Measurements (in mm) and indices: TL 6.20–7.98; HL 1.52–1.92; HW 1.68–2.00; EL 0.35–0.39; PW 1.48–1.80; PeW 0.58–0.75; PpW 0.61–0.80; HBaL 0.45–0.52; HBaW 0.15–0.17; CI 104.2–110.5; PI 111.1–113.5; PPeI 240.0–255.2; PPpI 225.0–242.6; HBaI 32.7–33.3.

G y n e (Fig. 294) (description of KEMPF, 1958 a). - "Total length 8.4–8.9 mm; maximum length of head 1.85–2.03 mm; of thorax 2.46–2.53 mm. Black; the following yellowish-brown: anterolateral portion of head disc (variable as regards extension, occasionally the entire rim of disc and the sides may be included), a narrow, elongate spot on the shoulder, usually (not always, variation i. e. absence of spots noticed in female specimens of a colony that usually have them!) four spots on the first gastral tergite, extensor face of tibiae. Scape and tarsites more or less fuscous-ferruginous.

Same diagnostic features as in soldier, excepting the following characteristics: Head disc distinctly more elongate. Shape of peduncular and epinotal teeth quite variable, not always as shown in fig. 14. Mesopleural tooth always present, but sometimes very small. Wings somewhat infuscated, veins brown. Venation of fore wing not significantly different from that of *liogaster*. Fore wing, when folded over the back, projects a little over the apex of the normally contracted gaster."

Wings as in Fig. 295.

Measurements (in mm) and indices: TL 7.32–9.04; HL 1.40–1.80; HW 1.48–1.72; EL 0.35–0.42; PW 1.44–1.68; PeW 0.59–0.63; PpW 0.68–0.87; HBaL 0.44–0.56; HBaW 0.16; CI 95.5–105.7; PI 102.4–102.8; PPeI 244.1–266.7; PPpI 193.1–211.8; HBaI 28.6–34.8.

M a l e (previously undescribed). - Head (eyes included, mandibles excluded) about 1/3 broader than long; vertexal margin straight, superficially carinate and diverging towards the sides. Vertex convex. Ocelli and compound eyes protuberant. Frontal carinae diverging backwards and not reaching the posterior border of the eyes. Frons flat. Clypeus convex, with impressed posterior border. Mandibles superficially carinate laterally. Scapes thick, twice as long as the first funicular joint.

Mesosoma. Pronotum in dorsal view with nearly parallel sides; mesonotum convex; median Mayrian and parapsidal furrows weakly impressed. Propodeum with well differentiate basal and declivous faces; basal face gently convex, medially sloping posteriorly; its sides converging posteriorly towards the declivous face, the latter with lateral and median carinae.

Petiole and postpetiole convex dorsally. Petiole narrower than the postpetiole and with a node deeply concave anteriorly; petiolar sides slightly convex. Postpetiolar sides convex.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 296.

Wings as in the gyne.

Legs stout.

Sculpture. Head dorsum minutely reticulate, with irregular, small foveae superimposed by sparse, irregular, longitudinal, thin rugosities, the rugosities transversal around the eyes. Ventral face of the head with the same sculpture as on the head dorsum but with denser foveae. Pronotum reticulate and with dense, irregular foveae. Mesonotum and scutellum superficially reticulate, with superimposed small, sparse and shallow foveae and with sparse, longitudinal rugosities. Basal face of the propodeum irregularly foveolate-rugulose. Declivous face of the propodeum superficially reticulate, shining and with few, short, longitudinal rugosities. Propleurae reticulate and with sparse, longitudinal, thin rugosities, denser on the ventral part. Mesopleurae with the same sculpture as on the mesonotum. Lower

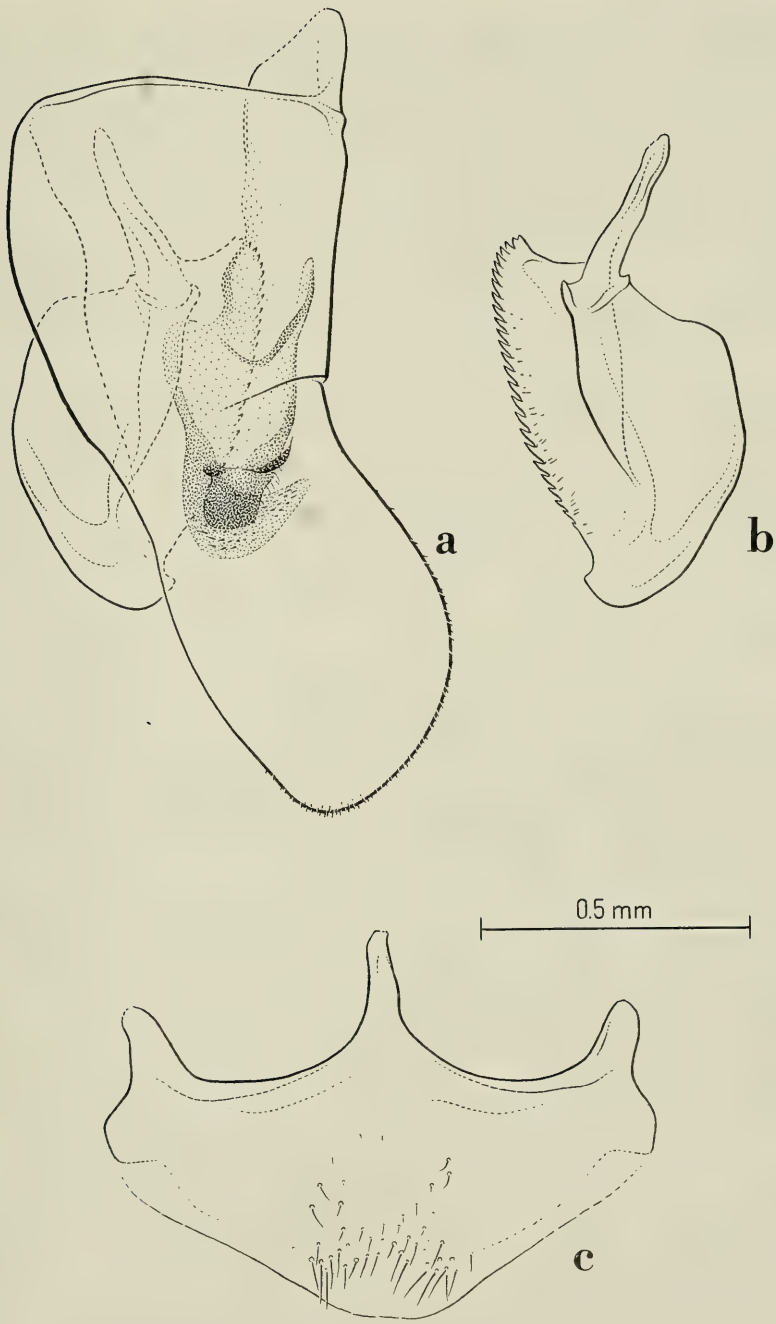


Fig. 296. *Cephalotes jheringi* (EMERY). Male from S. Felicia (Santa Fé), Argentina. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

metapleurae superficially reticulate and longitudinally rugulose; upper metapleurae reticulate and irregularly rugulose. Peduncular segments superficially reticulate and longitudinally rugulose, the rugosities more irregular on the petiole. First gastral tergite deeply reticulate; its anterior half with longitudinal rugosities originating from the postpetiolar articulation. Remaining tergites and sternites with superficial reticulation. Coxae and femora superficially reticulate, remaining parts of the legs simply punctate.

Pilosity. Body with dense, long, suberect, flexuous hairs, sparser and subdecumbent on the gaster, rare on the femora, absent on the tibiae and tarsi. Femora, tibiae and tarsi with decumbent hairs much shorter than the flexuous ones.

Colour. Black. Coxae and femora brown, distal parts of the legs lighter.

Measurements (in mm) and indices: TL 6.32; HL 0.92; HW 1.12; EL 0.47; PW 1.04; PeW 0.59; PpW 0.69; HBaL 0.61; HBaW 0.14; CI 121.7; PI 107.7; PPeI 176.3; PPpI 150.7; HBaI 22.9.

Material examined. - **Brazil**: Rio Grande do Sul: no further locality, 2 workers (syntypes of *jheringi*), JHERING [MCSN]; no further locality, 09.VII.1903, 1 worker, v. JHERING [MZSP]; Campinas nr. Erexim, XII.1954, 4 workers, G. MAZURANA [MZSP]; Nova Petrópolis, I.1928, 1 worker, 1 soldier, P. BUCK [MZSP].

Argentina: Formosa: Las Lomitas, VI.1948, 1 worker [MZSP]. Chaco: Resistência, 17.VI.1948, 1 worker [MZSP]; Col. Benitez, 7.XII.1948, 1 worker, GOLBACH [MZSP]. Catamarca: no further locality, 1 soldier (holotype of the unavailable name *jocans*), C. BRUCH [MHNG]; La Cienaga, Belén, 1926, 1 worker, WEISER & WOLTERS [MZSP]. Santiago del Estero: Tintina, 21.II.1920, 1 worker, Cornell University Exped. [USNM]. Tucumán: no further locality, I.1900, 2 workers [NHMB]; no further locality, 5 workers, 1 gyne [MZSP]; Tafi Viejo, 11.VIII.1952, 17.VIII.1954, 68 workers, 5 soldiers, 4 gynes, N. KUSNEZOV [MHNG, MCZC]; km 1333, Rte. 9, N of Tapia, 25.I.1967, forest Chaqueño, 4 workers, W. L. BROWN [MCZC]. Santa Fé: Rosario, in Weidenstamm, 3 workers, 2 soldiers, 1 gyne (syntypes of *ellenriederi*), [MHNG, ZSMC]; same locality, 1 worker, 1 soldier (without head), HUBRICH [MHNG, NHMB]; S. Felicia, 6 workers, 4 soldiers, 2 gynes, 3 males [MZSP]. Entre Ríos: La Picada, 5 workers, 1 soldier, N. KUSNEZOV [MCZC, MZSP]; Paraná, 5.VI.1951, 4 workers, 1 soldier [MZSP]; La Paz, 6.VI.1951, 2 workers, KUSNEZOV [MZSP]. Córdoba: Alta Gracia, in branches of cocos, 13 workers, 4 soldiers, 2 gynes (syntypes of the unavailable name *gaudens*), BRUCH [NHMB]; Alta Gracia, La Granja, Sierra de Córdoba, II.1922, 1 soldier (labelled as paratype of *gaudens*), C. BRUCH [MZSP]; same locality, 19.II.1925, 2 workers, 1 soldier, 1 male, C. BRUCH [MZSP]. Buenos Aires: Buenos Aires, 1 worker (erroneously labelled as syntype of *ellenriederi*) [MHNG]; same locality, 2 workers, G. A. BAER [MNHN]; Island Martin Garcia, 3 workers [MZSP]; San Isidoro, 2 workers, 2 soldiers [MZSP]; San Fernando, VII.1957, 35 workers, 13 soldiers, 3 gynes, DAGUERRE [USNM]; nr. La Plata, 16.I.1963, on flowers of *Aeschynomene montevidensis*, 1 worker, F. G. WERNER [MCZC].

Paraguay: San Salvador, 1 soldier, 1 gyne (syntypes of *peltatus*), BOHLS [MCSN]. La Cordillera: Asunción, VII.1961, 1 worker, N. L. H. KRAUSS [USNM].

Discussion. - *C. jheringi* is very similar to *bohlsi*. The characters useful to discriminate the two species have been already listed under *bohlsi*.

The *jheringi* material we examined suggests a high degree of variability of the three female castes.

Among workers, small specimens have the head narrower than long while the large ones have the head broader than long. The pronotal spines can be more or less pointed among specimens from the same nest. The type series of the unavailable name *gaudens* has the first pair of pronotal spines more salient and pointed than most other workers examined; a worker from Tintina (Santiago del Estero) has pronotal spines longer and less broad. The propodeum bears two or three pairs of spines, rarely four, in individuals of the same nest. The gastral lobes are normally

pigmented but in the type series of *gaudens* and in the specimens from Tafi Viejo (Tucumán) the lobes can be either pigmented or semitransparent.

The soldiers exhibit a great variability in colour. The head can be yellow to brown and rarely black. Some specimens with light coloured head may have a black clypeus. The pronotum can vary from completely yellow to brown with different combinations thereof. Small soldiers have the gaster either entirely black or with a pair of orange-brown spots on the posterior border of the first tergite. Large soldiers regularly have two pairs of well defined spots on the first gastral tergite.

The gynes equally show a great degree of variation in colour. Specimens from Tafi Viejo (Tucumán) have black head with yellow-orange frontal carinae while the rest of the gynes examined have yellow-brown head with or without darker clypeus. The pronotum follows the same colour variation pattern as in the soldiers. The four gastral spots can be present or absent according to the specimen.

The relatively long synonymic list of *jheringi* can be easily explained by means of the great variability observed in this species.

The syntype soldier and gyne of *peltatus* correspond to the general habitus of *jheringi* but are considerably smaller in size. KEMPF (1958 a) proposed the synonymy of the two species without actually examining the type material of either of them. We can now confirm entirely his judgement.

Distribution: Brazil, Argentina, Paraguay.

Cephalotes fossithorax (SANTSCHI) new combination
Figs. 297, 298

Cryptocerus fossithorax SANTSCHI, 1921 b: 125. Worker and soldier. Original description. Type locality: Viedna (Río Negro, Argentina). Type material: 4 syntypes (one soldier and three workers) in NHMB (examined); one syntype worker in MZSP (examined); several workers and soldiers from the same nest as the type in the collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (KEMPF, 1958 a), not available for the present study.

Paracryptocerus fossithorax SANTSCHI, KEMPF, 1958 a: 58, figs. 6, 9. Worker and soldier. First combination in *Paracryptocerus*.

Zacryptocerus fossithorax (SANTSCHI), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *fiebrigi* clade differing from its next outgroup species, *jheringi*, and from its next ingroup species, *supercilii*, in the worker, soldier and gyne by the erect, very short, truncate body hairs.

Worker (Fig. 297) (description of KEMPF, 1958 a). - "Total length 3.8–4.7 mm; maximum length of head 1.09–1.37 mm; of thorax 1.07–1.28 mm. Very close to *jheringi*, from which it differs by the ensemble of the following features:

Color reddish-brown; dorsum of body, especially of head, more or less infuscated; legs usually lighter, yellowish-brown. One specimen is nearly black, with fuscous-ferruginous legs. Shape of head variable, subquadrate to subrectangular (but cephalic index: 0.88 - 0.90, definitely above *bivestitus*, with which it agrees to some extent in the shape of the lateral thoracic crest). Sides of head slightly emarginate above eyes, especially in larger specimens, which also show an apparently more elongate head. Sides of pronotum usually, not always, little converging caudad, its border with a denticulate crest. This crest contains at least two of four distinct, acute, strong teeth, and inbetween theses teeth smaller denticles. All teeth are foliaceous. Sides of mesonotum either straight or weakly dentate. Mesoepinotal suture distinct only laterally, absent in the middle. Anterior corner of basal face of epinotum with an obtuse, smaller tooth, followed posteriorly by a larger triangular tooth. Inferior corner of declivous face angulate, or even dentate. Peduncular segments of equal width. Petiole with

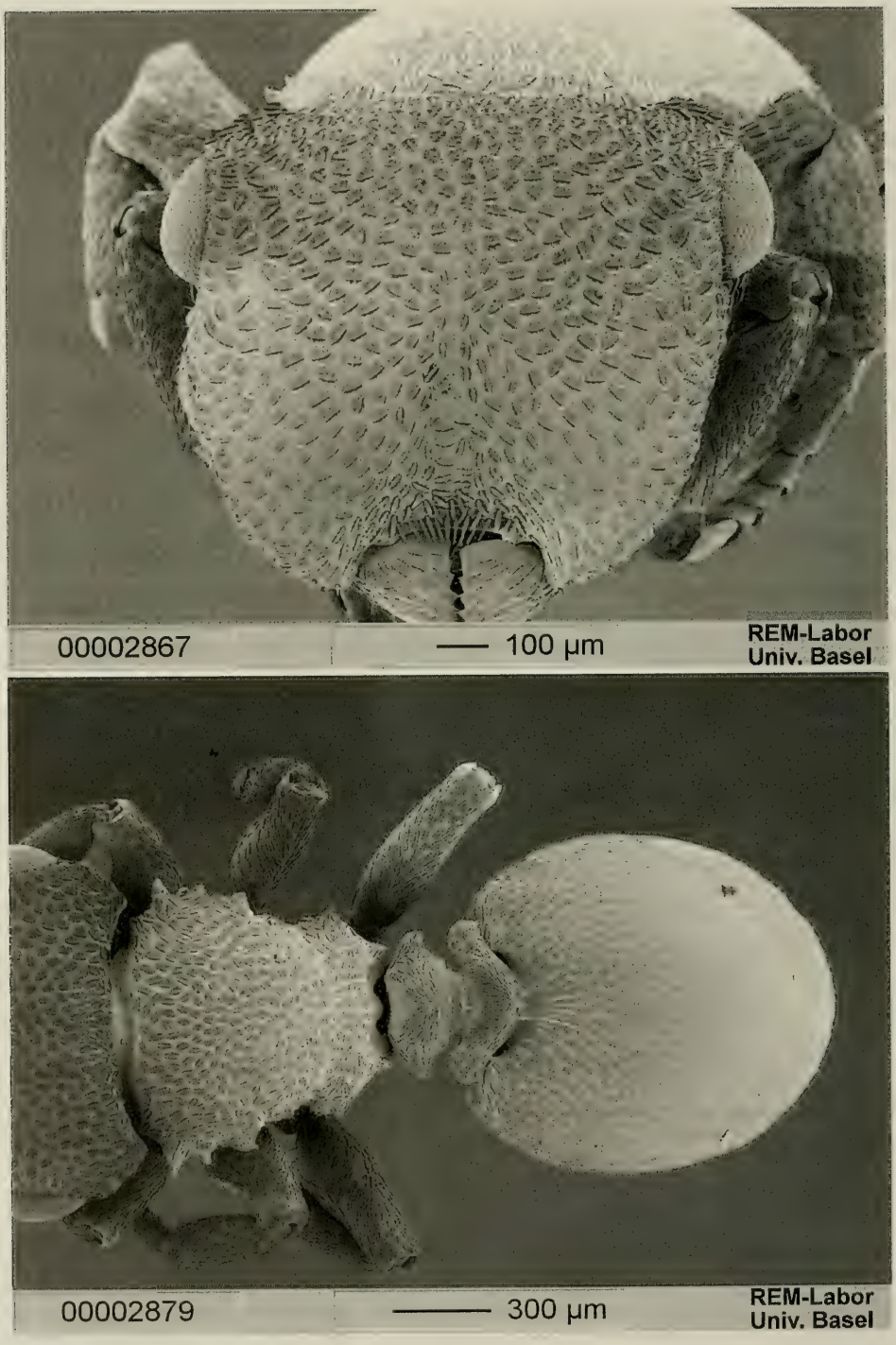


Fig. 297. *Cephalotes fossithorax* (SANTSCHI). Worker from Farga (San Luís), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

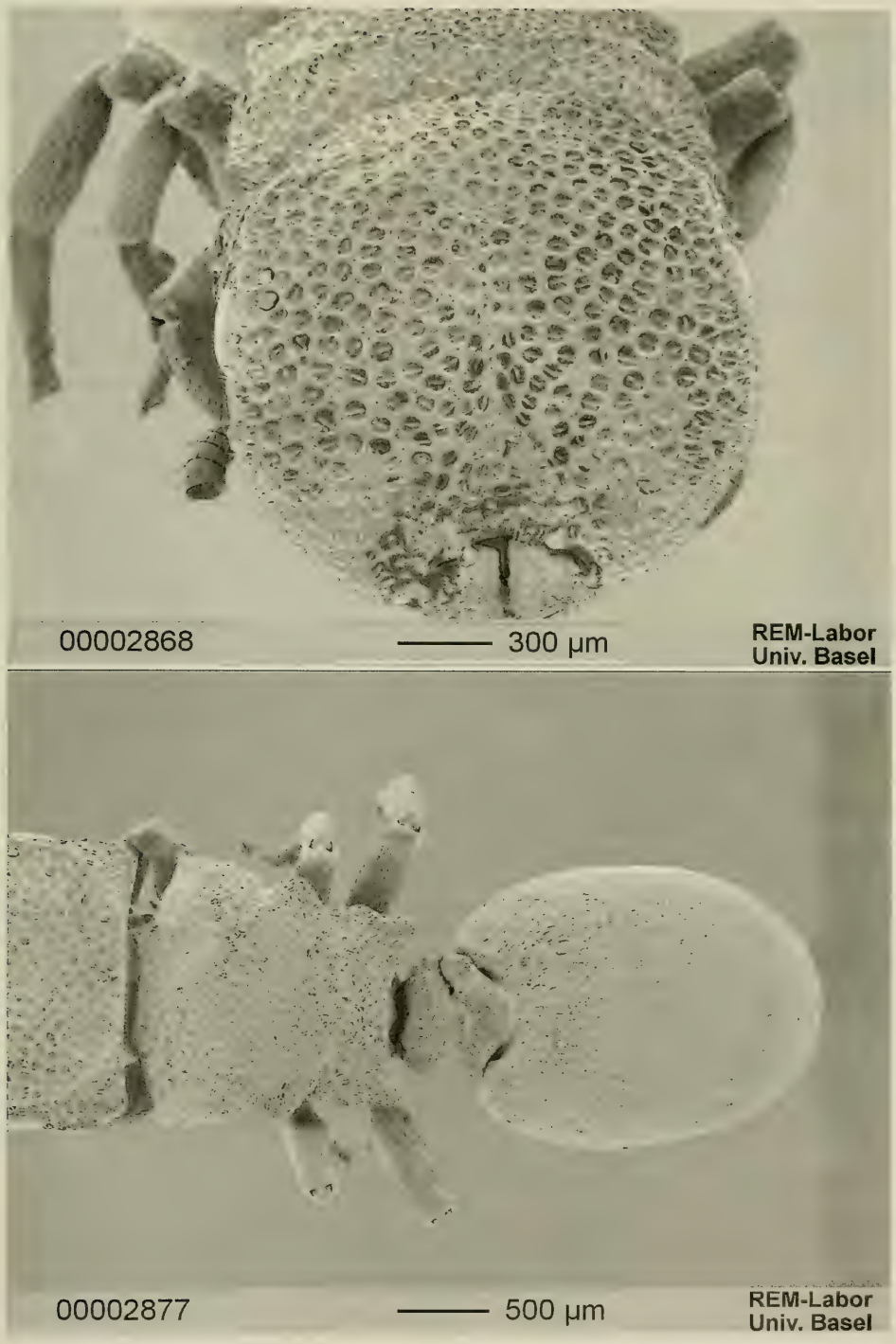


Fig. 298. *Cephalotes fossithorax* (SANTSCHI). Soldier from Farga (San Luís), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

strong lateral tooth, pointing obliquely backwards. Postpetiole with the customary lateral spines, the tips of which are rounded in front, and pointed behind. Postpetiole strongly convex dorsally. Anterolateral lobes of the usually rather short gaster thick, prominent, rounded, their borders at most very bluntly marginate, not depressed, nor forming a thin edge. Sculpture and pilosity not visibly different from *peltatus*."

Measurements (in mm) and indices: TL 3.77–4.36; HL 0.88–1.04; HW 0.98–1.14; EL 0.24–0.27; PW 0.83–0.97; PeW 0.47–0.51; PpW 0.40–0.51; HBaL 0.27.0.37; HBaW 0.09–0.11; CI 109.6–111.4; PI 117.5–118.1; PPeI 176.6–190.2; PPpI 169.4–190.2; HBaI 29.7–33.3.

S o l d i e r (Fig. 298) (description of KEMPF, 1958 a). - "Total length 6.5–7.3 mm; maximum length of head disc 1.75–2.10 mm; of thorax 1.71–1.86 mm. Likewise very similar to *jheringi*, except for the combination of the following features:

Black; anterolateral portion and lateral border of cephalic disc yellow to reddish-brown; a yellowish spot on each shoulder of the larger specimen. Gaster and legs fuscous-ferruginous. Head disc completely marginate, more or less rounded postero-laterally; lateral borders not raised, especially in larger specimen, which has the anterolateral portion of disc completely flat, not excavated. Clypeus with less pronounced teeth on the anterior border, its lateral sutures less distinct than in *jheringi*, not forming a prominent ridge. Foveolae of floor of head disc slightly more crowded than in *jheringi*, about 18 pits in a transverse row at the level of the eyes. Occipital lobes with a blunt tooth. Thorax with a transverse pronotal carina, which is not interrupted mesally in the larger worker. Apex of lateral mesonotal lobe not truncate, but subtriangular. Sides of basal face of epinotum without a prominent lateral lobe in larger specimen, with a triangular lobe in smaller specimen. Sculpture and pilosity much the same as in *jheringi*, with the exception of the projecting setulae on the rim of the head disc, which are fine and pointed at tip."

Measurements (in mm) and indices: TL 5.94–7.06; HL 1.44–1.72; HW 1.54–1.80; EL 0.32–0.36; PW 1.48–1.72; PeW 0.65–0.80; PpW 0.66–0.84; HBaL 0.37–0.43; HBaW 0.11–0.14; CI 1104.6–106.9; PI 104.0–104.6; PPeI 215.0–227.7; PPpI 204.8–224.2; HBaI 29.7–32.5.

G y n e (previously undescribed). - Head almost flat to slightly concave anteriorly and gently convex posteriorly, with disc. Sides of the disc strongly crenulate; posterior part of the sides of the disc converging before the eyes and connected with a faint, convex carina. Vertexal angles lower than the disc, convex and with crenulate border. Clypeal border concave. Mandibles carinate, the carina impressed. Dorsal border of the antennal scrobes with a crenulate carina ending in a small denticle before the eyes. Eyes convex and not hidden by the disc. Ocelli distant from the vertexal margin.

Mesosoma flat in side view. Pronotum anteriorly sloping. Humeral angles obtuse, their sides parallel. Pronotal carina superficially marked from the sides to the center where, in some specimens, it is interrupted by a superficial furrow. Promesonotal suture impressed. Mesonotum and scutellum on the same plane and flat. Propodeum with well differentiated basal and declivous faces. Basal face converging posteriorly and bearing a pair of small, round denticles or lobes and a pair of broad, round teeth slightly directed laterally. Declivous face gently concave on the sides and converging posteriorly.

Petiole with differentiated anterior and posterior faces; anterior face sloping; posterior face short. Sides of the petiole with a pair of short, round or obtuse denticles. Postpetiole broadly convex, in some specimens with a gentle concavity in the middle. Postpetiolar sides with a pair of thick, broad, anterior lobes bearing an obtuse denticle posteriorly.

Gaster oval, with a broad, protruding anterolateral lobe.

Hind femora neither angulate nor denticulate. Hind basitarsi more compressed apically than distally and without a broad base.

Sculpture. Head dorsum reticulate and covered by large foveae broader than their interspaces, or, in some specimens, contiguous each other. Frontal carinae with foveae shallower than those on the head dorsum. Sides of the head densely foveolate. Ventral part of the head with irregular foveae variably clumped and shaped as broad reticulation. Pronotum, scutellum and upper mesopleurae reticulate with superimposed dense foveae, less dense on the anterior part of the pronotum. Mesonotum, propleurae and lower mesopleurae reticulate, with superimposed sparse and shallow foveae. Basal face of the propodeum, posterior face of

the petiole, postpetiole reticulate-foveolate, the foveae agglomerate and irregular in shape. Declivous face of the propodeum and metapleurae reticulate and with faint, irregular, longitudinal rugosities, the same rugosities but rarer on the pro- and mesopleurae. Gaster, anterior face of the petiole and legs reticulate. Anterior half of the first gastral tergite and sternite and extensor face of the legs with irregular, longitudinal, anastomosing rugulosities which may or may not cover most of the first tergite. Gaster with sparse, small, piligerous foveae. Posterior half of the first gastral sternite and remaining sternites faintly reticulate and shining.

Pilosity. Each fovea with an appressed, short sensillum auricillicum. Legs and gaster apparently with the same appressed hairs as those in the foveae but thinner. Body with sparse, short, thin, suberect, truncate hairs, these hairs are very evident on each crenulation of the frontal carinae and on the sides of the body. Posterior borders of the gastral tergites and whole sternites with the same type of hairs as those on the crenulation of the frontal carinae but longer; rare, long and pointed hairs on the posterior border of the sternites.

Colour. Dark ferrugineous to light brown. Frontal carinae, sides of the head over the eyes, pronotal sides and extensor face of the tibiae yellowish-orange to light ferrugineous; remaining parts of the legs ferrugineous with darker tarsi. Gaster with two pairs of oval yellow spots, the first pair anterolateral, reaching the stigma, the second one on the postero-lateral third of the gaster but not reaching the border of the tergite. Body opaque with superficially shining head.

Measurements (in mm) and indices: TL 8.08–8.22; HL 1.48–1.52; HW 1.50–1.56; EL 0.34–0.36; PW 1.48–1.52; PeW 0.64–0.67; PpW 0.77; HBaL 0.43–0.45; HBaW 0.14–0.15; CI 101.3–102.6; PI 101.3–102.6; PPeI 220.9–237.5; PPpI 192.2–197.4; HBaI 32.5–33.3.

Material examined. - **Argentina**: without further locality, 2 workers [MCZC]. Santa Fé: Rosario, 4 gynes, W. M. Davis [MCZC]. Córdoba: Córdoba, 3 workers, 3 soldiers, 2 gynes, W. M. Davis [MCZC]; INTA Exp. Sta. near Manfredi, 2.XII.1967, in *Prosopis nigra*, 1 worker, C. R. Ward [USNM]. San Luís: Rt. 7, K 672, NW of Farga, 16.XII.1967, in *Prosopis caldenia*, 2 workers, 3 soldiers, C. R. Ward & E. W. Huddleston [USNM]. Río Negro: without further locality, 4 workers, 1 soldier (syntypes), Hildemann [MZSP, NHMB].

Discussion. - *C. fossithorax* appears to be an endemic Argentinean species. In Argentina its distribution overlaps the one of its two closest species, *jheringi* and *supercilii*.

Kempf (1958 a) doubted the distinctness of *fossithorax* because of the lack of characters separating it from *peltatus* (= *jheringi*) and *bohlsi*. We already mentioned in the diagnosis the body pilosity as a clear-cut character distinguishing *fossithorax* from *jheringi* and this character holds also for *bohlsi*. An additional character that can be used to distinguish *fossithorax* from *jheringi*, *supercilii* and *bohlsi* (the less similar among the three most closely related species) is the deeper body sculpture.

Distribution: Argentina.

Cephalotes supercilii de Andrade new species
Fig. 299

Cryptocerus peltatus Ellenriederi Forel, Forel, 1914: 281, partim. Misidentification.

Holotype: worker, Argentina, Rosario, W. M. Davis [MCZC].
Paratype: 1 gyne, same data as the holotype [MCZC].

Derivatio nominis: this species is named from the Latin *supercilium* (= eyebrow), referred to the long hairs on the border of the frontal carinae.

Diagnosis. - A member of the *fiebrigi* clade differing from its next outgroup species, *fossithorax*, in the worker by the sides of the frontal carinae with

erect, long, pointed hairs, and, in the soldier and in the gyne, by the same type of hairs but extended from the sides of the frontal carinae to those of the head.

W o r k e r (Fig. 299). - Head broader than long. Vertexal angles round. Vertexal margin concave. Frontal carinae not upturned over the eyes. Mandibles laterally carinate.

Mesosoma gently convex in side view. Scapular angles visible in dorsal view. Pronotum with a narrow lateral lamella with three pairs of irregular teeth, the first pair more pointed and the second and third ones more angulate. Sides of mesonotum with a pair of small teeth. Promesonotal suture superficially impressed. Propodeal suture weakly impressed. Propodeum with differentiate basal and declivous faces and with the sides narrowing backwards; sides of the basal face with two pairs of teeth, the first pair simply angulate and the second one larger and pointed; sides of the declivous face unarmed or with a pair of minute denticles.

Petiole anteriorly truncate; its anterior border superficially concave medially. Petiolar spines arising from the anterior face of the petiole, pointed and curved backwards. Postpetiole as broad as the petiole; its lateral expansions broad, developed anteriorly, curved and pointed backwards.

Gaster suboval, with a pair of broad, anterolateral lobes.

Mid and hind femora not angulate; mid and hind basitarsi flat and with subparallel sides.

Sculpture. Body minutely reticulate, the reticulation less impressed on the posterior half of the first gastral sternite which is shining. Head, mesosoma, pedicel, gaster and outer face of the femora and of the tibiae foveolate, the foveae larger on the posterior third of the head dorsum and on the pronotum, sparser on the frons, shallower on the frontal carinae, irregular on the ventral part of the head, absent on the upper pleurae, more oval and superficial on the pedicel, on the gaster and on the legs. Ventral part of the head and lower propleurae with additional irregular, longitudinal, thin rugosities.

Pilosity. Body with three types of hairs: (1) appressed and generally originating from each fovea, of size proportional to the one of the respective fovea, i. e. larger on the posterior third of the head dorsum and on the pronotum, shorter and thinner on the body parts without foveae; (2) pointed, long on the border of the frontal carinae, sparse on the gastral sternites, rare on the coxae and on the ventral face of the femora; similar but slightly longer and rare hairs on the posterior borders of the second and third gastral sternites; (3) short, truncate and rare on the posterior border of the remaining gastral tergites and on the legs.

Colour. Black, gaster and legs lighter. Frontal carinae, mesosomal and peduncular spines and outer face of the tibiae yellowish to light brown.

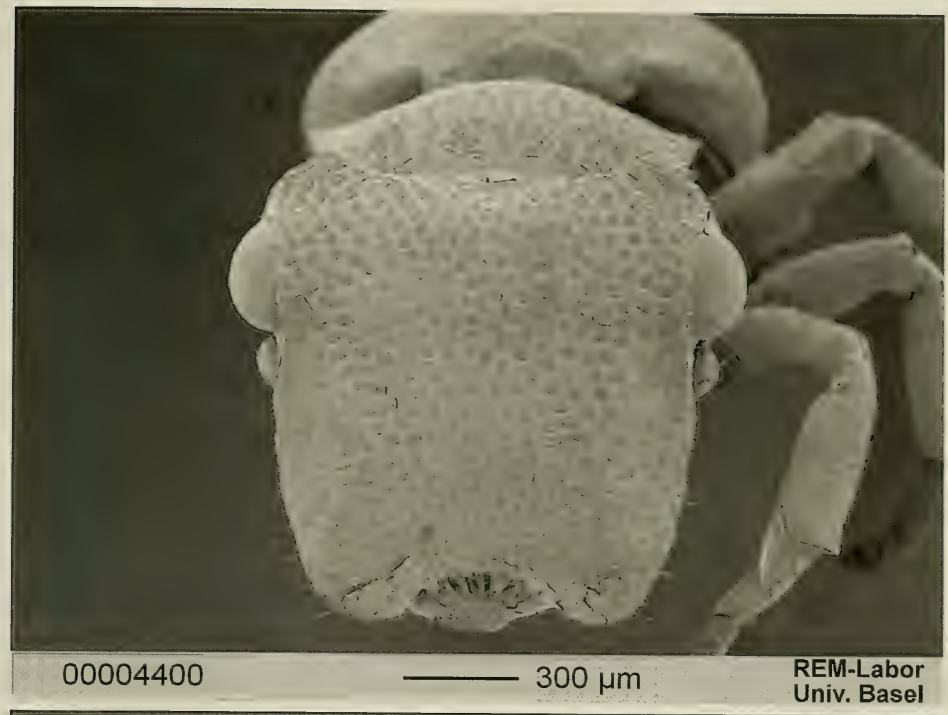
Measurements (in mm) and indices: TL 4.48–4.52; HL 1.04–1.06; HW 1.12; EL 0.29–0.30; PW 1.00; PeW 0.56–0.58; PpW 0.54–0.59; HBaL 0.39; HBaW 0.10; CI 105.7–107.7; PI 112.0; PPeI 172.4–178.6; PPpI 169.5–185.2; HBaI 25.6.

S o l d i e r . - Head slightly broader than long, with complete disc. Floor of the disc gently convex posteriorly and slightly concave anteriorly. Frontal carinae and borders of the disc strongly crenulate and weakly raised only anteriorly. Sides of the disc narrowing backwards, not hiding the eyes. Posterior border of the disc convex. Vertexal angles broad, convex and with an obtuse tooth internally. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a longitudinal, denticulate carina just in front of the eyes.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of small denticles. Pronotal sides weakly convex. Pronotal crest marked, thickening from the sides towards the center, where it is interrupted by a sulcus. Promesonotal suture superficially impressed. Sides of the mesonotum with a broad, obtuse tooth bearing a narrow, superficial impression. Propodeal suture impressed. Propodeum with well differentiate basal and declivous faces. Sides of the basal face with a small pair of short, broad, subtriangular teeth and with a pair of large, stout teeth curved upwards. Declivous face medially concave; its sides converging and weakly carinate laterally.

Petiole with the anterior face oblique and medially concave; its sides with a pair of pointed spines curved backwards. Postpetiole convex. Postpetiolar sides with a pair of thick, round expansions arising from the anterior border, directed anterolaterally and pointed backwards.

Gaster oval and with a pair of anterolateral lobes.



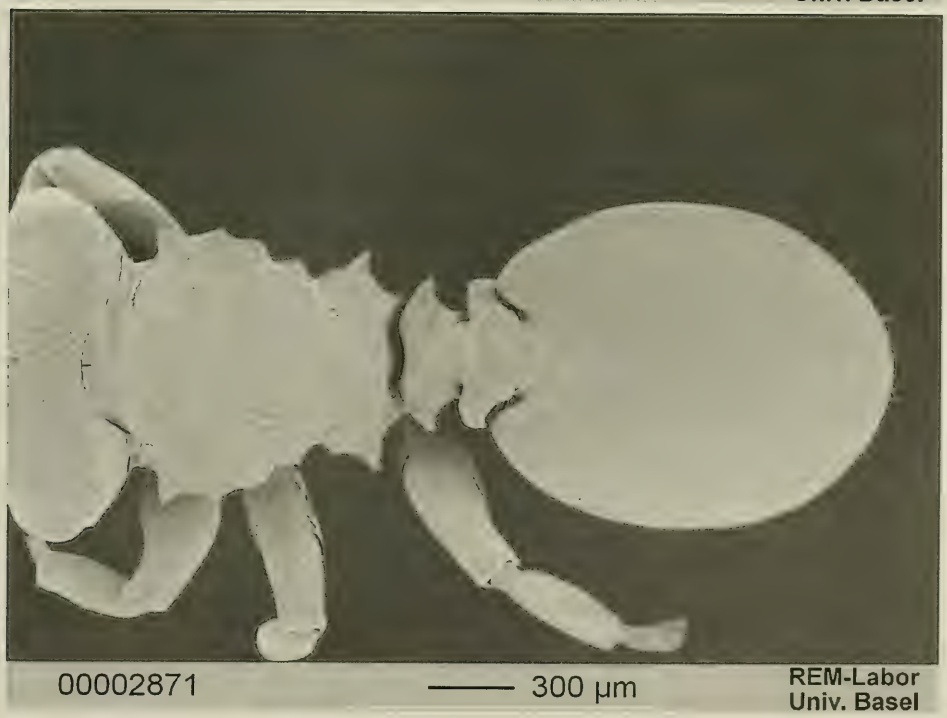


Fig. 299. *Cephalotes supercilii* DE ANDRADE. Worker from Argentina (no further locality): head (top) and meso- and metasoma (bottom) in dorsal view.

Mid and hind femora without angle or denticle. Hind basitarsi with subparallel sides.

Sculpture. Head, mesosoma and pedicel minutely reticulate-punctate, superficially shining and foveolate, the foveae contiguous on the head dorsum and on the mesosoma, irregular, large and deep on the head dorsum only, shallow and sparse on the ventral part of the head, oval on the lower meso- and metapleurae and on the pedicel, absent on the upper metapleurae and on the declivous face of the propodeum. Lower pro- and metapleurae with additional thin rugosities. Gaster and legs reticulate, the reticulation less impressed on the posterior half of the first gastral sternite, shining. Anterior third of the first gastral tergite and outer face of the femora and tibiae with superficial, oval foveae, larger on the on the tergite. Anterior third of the first gastral tergite close to the postpetiolar articulation and sides of the anterior half of corresponding sternite also with few, longitudinal rugosities.

Pilosity. Body with six types of hairs: (1) canaliculate, subdecumbent to decumbent originating from most of the foveae on the head dorsum, appressed and originating from each fovea on the other body parts; similar hairs but shorter and thinner on the parts without foveae; (2) pointed, long and flexuous on the border of the frontal carinae and on the sides of the head; (3) subtruncate, erect and originating from the remaining foveae of the head dorsum not bearing type (1) hairs, sparse on the gastral sternites, rare on the coxae and on the lower femora; (4) longer than the hair type (2) and rare on the posterior borders of the second and third gastral sternites; (5) truncate on the posterior border of the gastral tergites; (6) subclavate and rare on the legs.

Colour. Dark brown, gaster and legs lighter. Head dorsum and superior part of the sides dark orange to light brown, frontal carinae yellow. Pronotal sides with a light brown strip.

Measurements (in mm) and indices: TL 7.58; HL 1.80; HW 1.88; EL 0.37; PW 1.80; PeW 0.73; PpW 0.78; CI 104.4; PI 104.4; PPeI 246.6; PPpI 230.8.

Gyne. - Differing from the soldier, besides than in the usual caste-dependent traits, in the following details:

Head almost as broad as long. Floor of the disc more convex posteriorly and flat anteriorly. Vertexal angles simply angulate medially. Humeral angles simply angulate. Pronotal sides straight. Mesonotum and scutellum flat. Sides of the basal face with a small pair of short, round denticles and with a pair of large, stout teeth, slightly diverging and directed backwards. Petiolar sides with a pair of very small denticles. Postpetiolar spines less developed and smaller. Gaster longer and with more protruding lobes.

Sculpture. Foveae denser on the ventral part of the head, less regular and sparser on the mesosoma Propleurae with denser rugosities.

Pilosity. Head dorsum with hair types (1) and (2) almost in the same proportions. Mesosoma, pedicel, first gastral tergite and legs with rare, subtruncate hairs of type (2). Posterior border of the gastral tergites with denser hairs of type (4)

Colour. As in the soldier except for the presence of a pair of yellow spots close to the posterior border of the first gastral tergite.

Measurements (in mm) and indices: TL 9.06; HL 1.70; HW 1.72; EL 0.38; PW 1.72; PeW 0.69; PpW 0.85; HBaL 0.50; HBaW 0.16; CI 101.2; PI 100.0; PPeI 249.3; PPpI 202.3; HBaI 32.0.

Material examined. - **Argentina**: without further locality, 1 worker [MCZC]. Santa Fé: Rosario, 1 worker (holotype) 1 gyne (paratype), W. M. Davis [MCZC]. Córdoba: Córdoba, 1 soldier, W. M. Davis [MCZC]. San Luís: Represa del Carmen, Alto Pencoso, in a branch of *Prosopis*, 1 worker, C. Bruch [MHNG].

Discussion. - *C. supercilii* is similar to another Argentinean species, *fossithorax*. Both species, *supercilii* and *fossithorax*, appear to be sympatric over the entire area of the first (Córdoba and Rosario).

The unique soldier of *supercilii* has the mesonotal sides with the same integumental pits already known from *fossithorax*, although much smaller. Santschi (1921 b) used the presence of the pits as specific character for *fossithorax*, the character from which the name *fossithorax* is derived. Kempf (1958 a) considered the pits in ques-

tion as teratological. The teratological explanation appears to be reasonable since most other specimens of *fossithorax* are without integumental pits. The discovery of a soldier of the closest related species (*supercilii*) with similar pits, however, adds unanswered questions about the true nature of these structures.

One of the two workers from San Luís identified as *ellenriederi* by FOREL (1914) must be referred to *supercilii* (the other one is *bivestitus*).

Distribution: Argentina.

Cephalotes pilosus (EMERY) new combination
Figs. 300, 301, 302, 303, 304, 305

Cryptocerus pilosus EMERY, 1896: 630, fig. B. Worker and soldier. Original description. Type locality: San Salvador (Paraguay). Type material: lectotype worker (designated by KEMPF, 1958 a: 20) labelled: first label (handwriting of EMERY) "*Cryptocerus pilosus* Em, n. sp.", second label "*Paracryptocerus* (*H.*) *pilosus* (Emery), Lectotype", third label (typewritten) "*Paracryptocerus pilosus* record in type book under 60990", in the USNM; 2 soldiers, 2 small soldiers and 5 workers (all paratypes) labelled "Paraguay, Bohls" in MCSN, and 2 workers and 1 soldier (all paratypes) labelled "*Cryptocerus pilosus* Em., Paraguay", in MHNG, all examined.

Paracryptocerus pilosus (EMERY), KEMPF, 1958 a: 20, figs. 2, 8, 19, 20. Worker, soldier and gyne. First combination in *Paracryptocerus*.

Zacryptocerus pilosus (EMERY), BRANDÃO, 1991: 387. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *fiebrigi* clade differing from *lanuginosus* and *liogaster* by its denser, long, flexuous body hairs.

Worker (Fig. 300) (description of KEMPF, 1958 a). - "Total length 4.1–4.9 mm; maximum length of head 1.11–1.39 mm; of thorax 1.21–146 mm. Black; the following fuscous-ferruginous: tips of mandibles, scape, last funicular segment, femora, tibiae, the four distal tarsites; frontal carinae testaceous.

Head rather shining, subquadrate. Lateral borders scarcely sinuous, not raised above eyes, slightly diverging caudad. Dorsum of head moderately convex discally. Occipital lobes obliquely truncate, not transparent, their border irregularly crenate or notched. Occipital border broadly, but feebly, emarginate. Eyes hemispherical, bulging, their maximum diameter about one fourth of maximum head length. Frontal carinae semitransparent, in lateral view not considerably thickened just in front of the eyes.

Thorax longer than broad. Scapular angle feebly dentate, distinct from the first, acute lateral pronotal tooth, which is very conspicuous and followed posteriorly by a sharp lateral crest, on which two more, rather obtuse, teeth are apparent. Promesonotal suture obsolete. Mesonotum projecting laterad as a rectangular tooth. Mesoepinotal suture often, not always, visible, especially laterad (practically absent in the lectotype). Anterior corner of basal face of epinotum in the form of a small, more or less obtuse tooth, followed by a much larger, acute lateral tooth. Lateral border of declivous face with a rather sharp, often somewhat denticulate edge. In profile, the thorax is moderately convex, forming an even curvature, scarcely interrupted by the transition of the basal into the declivous face of epinotum. Femora fusiform, tibiae more or less cylindrical.

Petiole narrower than mesonotum, having on each side a small spine, curving obliquely caudad. Postpetiole slightly broader, the lateral spines stouter, their tips more recurved. In profile, the postpetiole is strongly convex above.

Gaster elliptical, broadly excised antero-mesially, its anterolateral lobes bluntly marginate.

Integument, with the exception of the gaster, rather shiny. Dorsum of head, thorax and pedicel reticulate-rugose and foveolate. Frontal carinae finely punctate. Mandibles finely rugose. Sides of fore coxae and laterotergite of pronotum horizontally striate. First gastral tergite finely but sharply punctate, opaque, with more or less longitudinal rugosities on the anterior half, and elongate, small shallowly impressed squamiferous pits scattered throughout. First gastral sternite shinier, superficially reticulate-punctate.

Canaliculate, long, appressed scalelike hair on head, thorax, and pedicel; similar hair, yet simple and small on first gastral tergite. Long, flexuous, standing hair scattered over the entire body and appendages, scarce on the sides of thorax, absent latero-ventrally on peduncle."

Measurements (in mm) and indices: TL 4.50–5.28; HL 1.04–1.24; HW 1.08–1.40; EL 0.29–0.32; PW 1.00–1.24 PeW 0.54–0.62; PpW 0.56–0.64; HBaL 0.44–0.48; HBaW 0.12–0.14; CI 103.8–112.9; PI 105.3–111.1; PPeI 178.6–211.1; PPpI 178.6–196.8; HBaI 27.3–31.8.

S o l d i e r (Fig. 301) (description of KEMPF, 1958 a). - "Total length 5.9–7.6 mm; maximum length of head 1.64–2.14 mm; of thorax 1.64–207 mm. Black; the following fuscous-ferruginous: anterolateral portions of head disc, tips of mandibles, scapes, last funicular segment, the anterior corner of pronotum; fuscous testaceous: extensor face of tibiae. Gaster with a pair of small anterolateral and another pair of slightly larger postero-lateral yellowish spots, which, however, are absent in smaller specimens.

Head slightly longer than broad (largest specimen 60:58, smallest 46:44). Head disc subquadrate, with strongly rounded corners, its bottom slightly convex discally, feebly excavate anterolaterally, its lateral border scarcely upturned, but strongly crenulate. Sides of disc almost straight, the occipital border strongly and rather evenly curved. Supramandibular excision broad and bidentate. Occipital lobes feebly obliquely truncate, with a small tooth on the inner end of the truncation. Eyes rather flat.

Thorax usually as broad as long. Pronotum laterally bidentate, with a distinct, crenulate, transverse crest, which is broadly interrupted mesally. Mesonotum with a bluntly rounded and submarginate lateral lobe. Mesoepinotal suture impressed. Basal face of epinotum with an obtusely angulate lobe on each side and on each posterior corner there is a strong, usually blunt, tooth, pointing upward and laterad. Lower half of slightly excavate declivity with a sharp lateral crest. Mesopleura with a blunt vestigial tooth near its antero-ventral corner. Legs as in worker, femora more incrassated, less distinctly fusiform.

Pedicel as in worker. Lateral spines of petiole and postpetiole stouter and more recurved. Gaster as in worker.

Integument less shining than in worker. Head disc, occiput and mandibles sharply reticulate-rugose with crowded, deeply impressed pits within the meshes of the anastomosing rugosities. Sculpture more superficial over the antennal scrobe. Sides of head and lower face coarsely foveolate with the intervals finely reticulate-punctate. Thorax and pedicel sculptured as head disc, the foveolae less crowded. On the laterotergite of pronotum there prevail longitudinal and somewhat curved rugosities. Gaster opaque, sculpture as in worker. Pilosity, in general as in worker. Each foveola of head disc bears a rather thin squamiform hair, which is more or less decumbent, and does not project beyond the rim of the pit. Scalelike hair of thorax and femora more conspicuous. Long, thin, flexuous standing hair around the rim of head disc, present also on the sides of head, occipital lobes, dorsum of thorax, peduncle and gaster, as well as on legs."

Measurements (in mm) and indices: TL 6.76–7.64; HL 1.72–1.96; HW 1.80–2.08; EL 0.33–0.39; PW 1.80–2.00; PeW 0.80–0.84; PpW 0.85–0.88; HBaL 0.44–0.52; HBaW 0.16–0.17; CI 104.2–106.1; PI 100.0–104.3; PPeI 219.0–265.0; PPpI 209.1–230.8; HBaI 31.9–36.4.

G y n e (Fig. 302). - Head broader than long, with a complete disc. Floor of the disc convex posteriorly, flat or gently concave anteriorly. Frontal carinae and borders of the disc strongly crenulate and weakly raised anteriorly. Sides of the disc subparallel, not hiding the eyes in dorsal view and connected by a convex border less marked in correspondence with the angles. Vertexal angles convex and with crenulate border. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a longitudinal, denticulate carina just in front of the eyes, the carina sometimes crenulate after the denticle.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of small denticles. Pronotal sides weakly convex. Pronotal carina superficially marked. Mesonotum and scutellum flat. Propodeum with well differentiate basal and declivous faces. Sides of the basal face with a small pair of short, obtuse denticles and with a pair of large, stout teeth slightly diverging and directed backwards. Declivous face concave in the middle; its sides converging posteriorly and carinate.

Fig. 300. *Cephalotes pilosus* (EMERY). Worker from Nova Europa (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

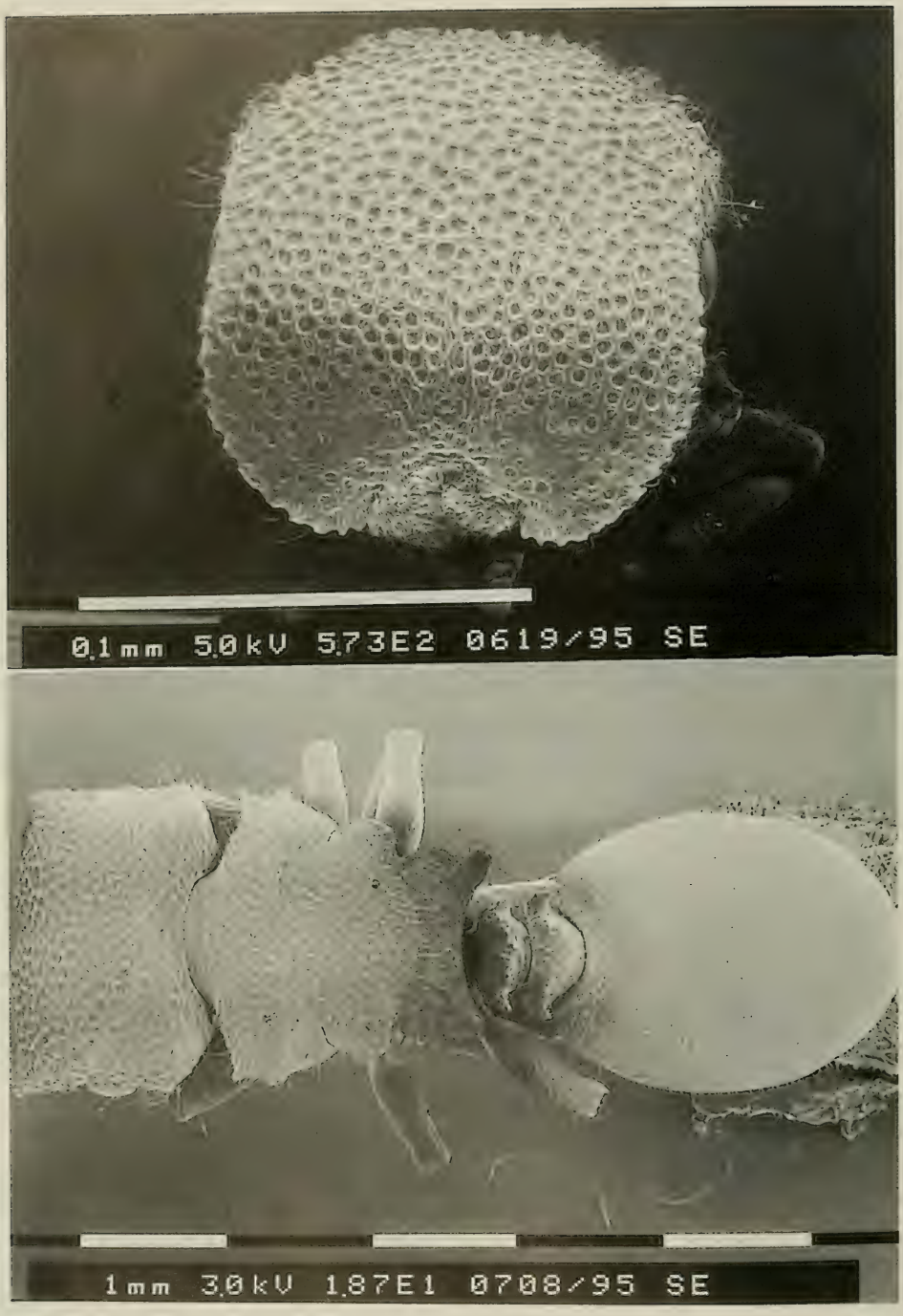


Fig. 301. *Cephalotes pilosus* (EMERY). Soldier from Nova Europa (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

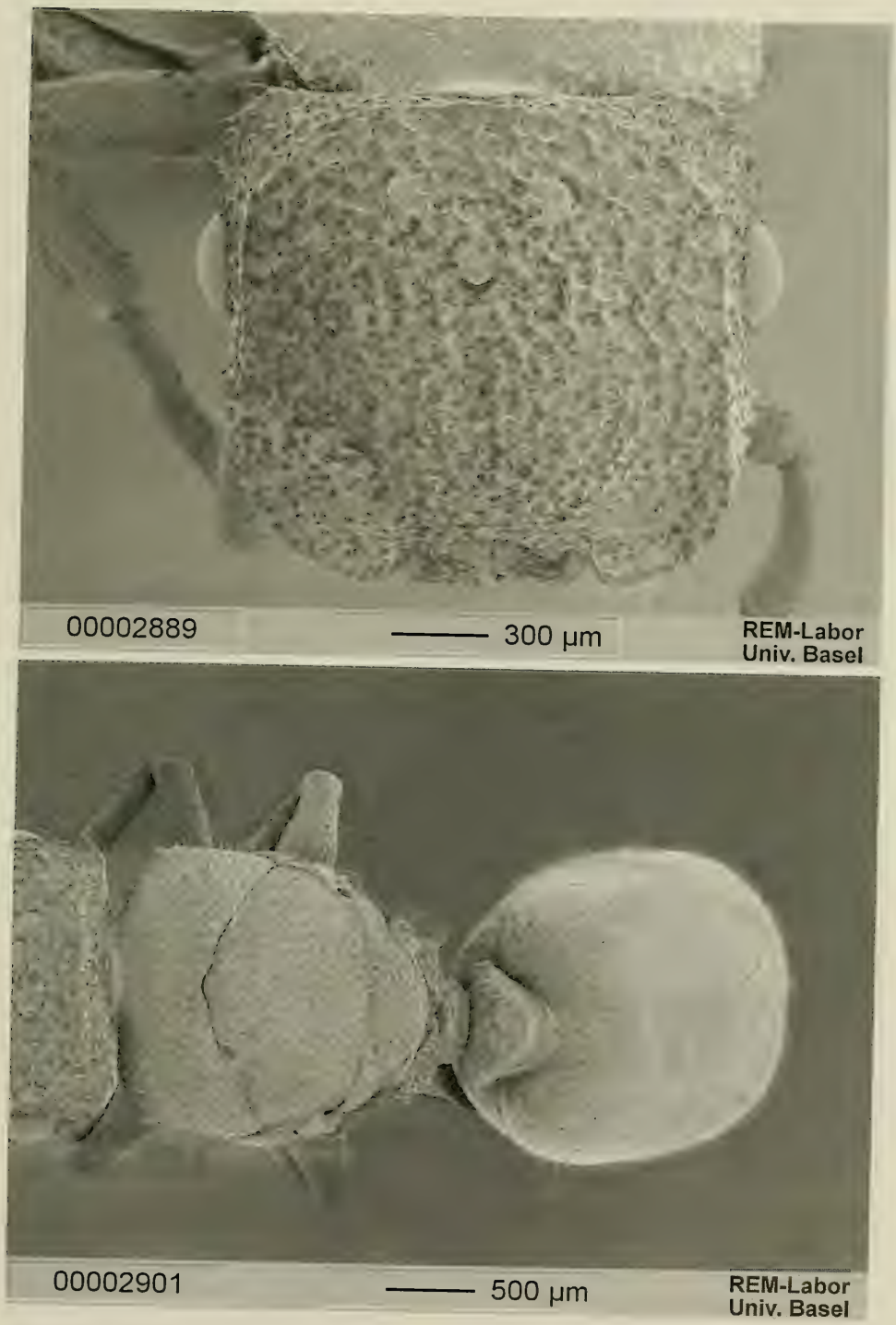


Fig. 302. *Cephalotes pilosus* (EMERY). Gyne from Botucatu (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Petiole with the anterior face oblique and gently concave medially; its sides with a pair of small denticles curved backwards. Postpetiole convex and with a "U" shaped carina. Postpetiolar sides with a pair of little developed, round expansions arising from the anterior border and pointed backwards.

Gaster with a pair of anterolateral lobes not strongly protruding anteriorly.

Mid and hind femora without angles or denticles. Hind basitarsi with subparallel sides.

Wings as in the male.

Sculpture. Head, mesosoma and pedicel minutely reticulate-punctate and with contiguous foveae, the foveae larger on the head, more regular on the pronotum, on the mesonotum and on the scutellum, more impressed on the head dorsum and on the propodeum. Foveae of the ventral part of the head and on the pleurae superimposed to irregular, longitudinal rugosities, except those on the upper mesopleurae. Gaster and legs reticulate, the reticulation less impressed on the posterior half of the first gastral sternite, shining. Anterior fourth of the first gastric tergite, outer face of the femora and tibiae with superficial, small, oval foveae. Anterior third of the first gastral tergite and sides of the anterior half of corresponding sternite with few, longitudinal rugosities.

Pilosity. Body with three types of hairs: (1) originating from part of the foveae, canaliculate, suberect, on the head dorsum, appressed on the other body parts; similar but shorter and thinner on the parts without foveae; (2) pointed, long and flexuous originating from foveae of the head, of the mesosoma, of the pedicel and of the gaster, and present also on the parts of the gaster and of the legs without foveae, but slightly shorter, on the first gastral tergite.

Colour. Black. Frontal carinae and pronotal sides yellow-brown. First gastral tergite with a small pair of dark yellow spots behind the lobes.

Measurements (in mm) and indices: TL 8.26–8.34; HL 1.52–1.56; HW 1.62–1.64; EL 0.33–0.35; PW 1.60–1.52; HBaL 0.50–0.54; HBaW 0.16; PeW 0.65–0.66; PpW 0.74–0.77; CI 105.1–106.6; PI 102.5–106.6; PPeI 233.8–242.4; PPpI 205.4–207.8; HBaI 29.6–32.0.

M a l e (Fig. 303) (previously undescribed). - Head (eyes included, mandibles excluded) about 1/3 broader than long; vertexal margin straight, faintly carinate and continuing with a round angle into the sides. Vertex convex. Ocelli protuberant. Eyes broadly convex and placed in the middle of the sides of the head. Frontal carinae diverging backwards and not reaching the posterior border of the eyes. Frons flat and separate from the clypeus by a furrow. Clypeus convex. Mandibles short, superficially carinate laterally and with a single distinct apical tooth. Scapes thick, twice as long as the first funicular joint.

Mesosoma. Pronotum in dorsal view with nearly parallel sides; mesonotum convex; median Mayrian carina and parapsidal furrows weakly impressed; scutellum convex, its sides converging posteriorly; propodeum with well differentiate basal and declivous faces; basal face gently convex and sloping posteriorly, its sides converging posteriorly towards the declivous face, the latter with lateral and median carinae.

Petiole as broad as or slightly narrower than the postpetiole and with an anteriorly deeply concave node; petiolar sides slightly convex. Postpetiole gently convex dorsally; postpetiole, in dorsal view, in form of an inverted trapeze.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 304.

Wings (Fig. 305). Fore wings with *R+Sc* superficially connected to a marked pterostigma. *cu-a* superficially connected with *A*. *2r* marked, *Rsf5* connected to *R1*. Distal parts of *A*, *Cu-A1* and *Mf4* less pigmented. Hind wings with *R*, *M+CuA*, *M* and *1A* marked; distal part of *M* and *CuA* vestigial.

Sculpture. Head dorsum reticulate, with irregular, small foveae superimposed by few rugosities. Eyes surrounded by transversal rugosities. Ventral face of the head with the same sculpture as on the head dorsum but with denser foveae and longitudinal rugosities. Pronotum reticulate, with more irregular foveae and rugosities. Mesonotum and scutellum superficially reticulate, with superimposed small, sparse and shallow foveae and with few longitudinal rugosities more impressed on the scutellum. Propodeum with broad, irregular, deep reticulation. Propleurae reticulate and with irregular, thin, rugulae. Mesopleurae with the same sculpture as on the mesonotum, but the rugosities on its posterior part only. Lower

Fig. 303. *Cephalotes pilosus* (EMERY). Male from Nova Europa (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

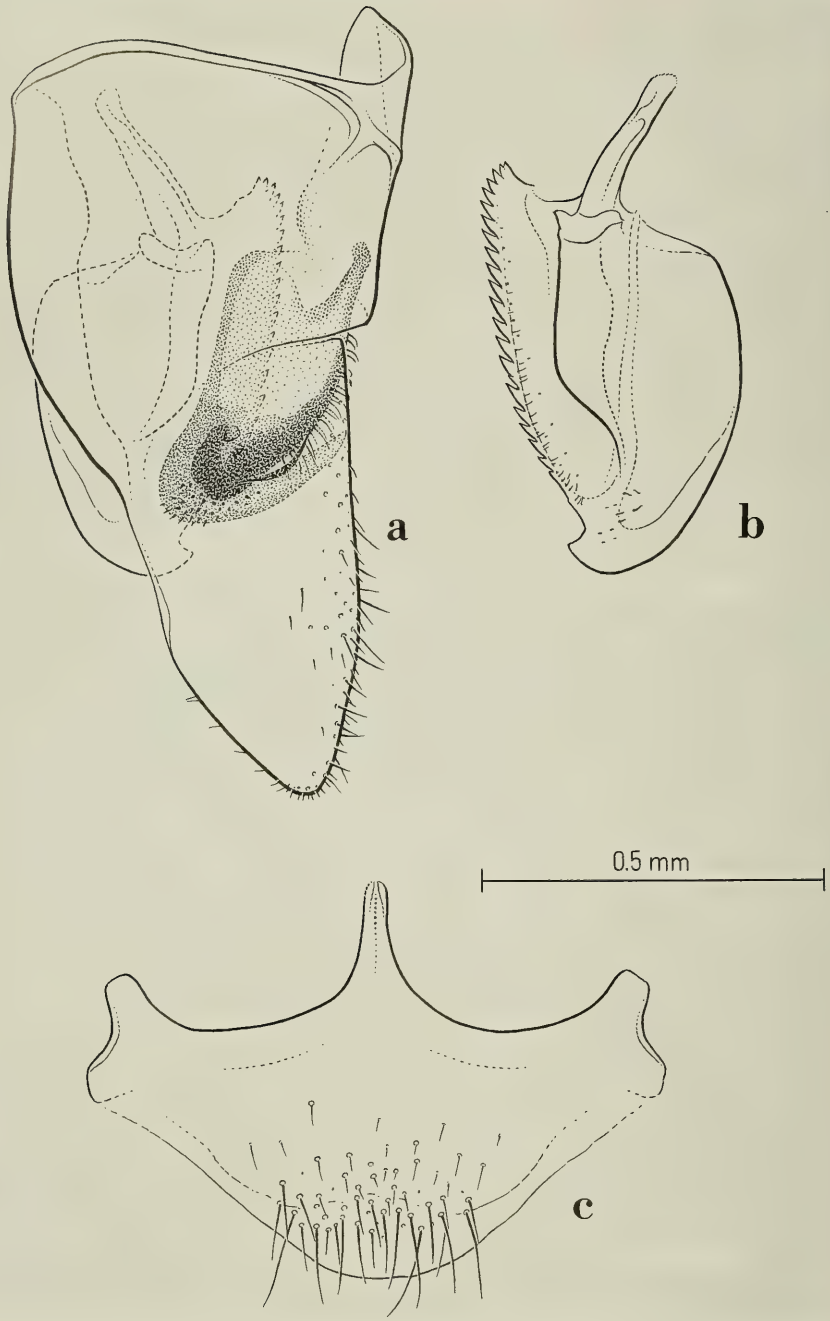


Fig. 304. *Cephalotes pilosus* (EMERY). Male from Nova Europa (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Fig. 305. *Cephalotes pilosus* (EMERY). Male from Nova Europa (São Paulo), Brazil, fore and hind wings.

Lower metapleurae superficially reticulate and longitudinally rugulose; upper metapleurae reticulate and irregularly rugulose. Peduncular segments superficially reticulate and longitudinally rugulose. First gastral tergite deeply reticulate and with sparse piligerous foveae; its anterior half with longitudinal rugosities. Remaining tergites with the posterior border broadly reticulate and with piligerous foveae. First gastral sternite with the same type of sculpture as on the first tergite but less impressed. Extensor face of the legs reticulate; anterior and posterior faces of the legs superficially reticulate to shining.

Pilosity. Body with dense, long, suberect, flexuous hairs; these same hairs but decumbent, sparser and shorter on the tarsi. Funiculi densely covered by thin, short, decumbent hairs; similar hairs on the internal face of the tibiae and on the tarsi.

Colour. Black. Apex of femora, tibiae and tarsi yellowish-brown.

Measurements (in mm) and indices: TL 5.80–6.20; HL 0.8–0.88; HW 1.04–1.12; EL 0.40–0.44; PW 1.04–1.16; PeW 0.52–0.54; PpW 0.52–0.58; HBaL 0.48–0.54; HBaW 0.11–0.12; CI 123.8–127.3; PI 96.5–103.7; PPeI 192.6–223.1; PPpI 179.3–207.7; HBaI 22.2–22.9.

Material examined. - **Brazil:** Rio Grande do Norte: Natal, 5 workers, 8 soldiers, 4 males, W. M. MANN [USNM]. Bahia: Itaberaba, Fazenda Riacho do Uruçu, 01–05.XII.1990, 4 workers, 13 soldiers, C. R. F. BRANDÃO et al. [MZSP]. São Paulo: Agudos, VII.1954, 1 worker, R. MÜLLER [MCZC]; same locality and collector, V.1958, 01.VI.1958, VIII. 1958, IX. 1958, 10 workers, 1 soldier [MZSP]; same locality 12.III.1952, 1 worker, W. W. KEMPF [MZSP]; same locality and collector, 03.X.1954, 12.XII.1954, 25.I.1955, 18 workers, 4 soldiers, W. W. KEMPF [MCZC, MZSP]; Anhembi, Fazenda B. Rico, 14.II.1969, 6 workers, 1 soldier, J. C. MAGALHÃES & M. KUHLANN [MZSP]; Nova Europa, Fazenda Itaquerê, 24.VIII.1963, 8 workers, 10 soldiers, 10 males, K. LENKO [MZSP]; Bálsamo, 09.VII.1972, 3 workers, J. M. DINIZ [MZSP]; Botucatu, 28.I.1996, 29 workers, 9 soldiers, 3 gynes, 3 males, M. L. DE ANDRADE [CPCC, INPA; MNHN, ZSMC, LACM, NHMB].

Paraguay: San Salvador, 1 worker (lectotype, without locality label) [USNM], 7 workers, 5 soldiers (all paralectotypes), BOHLS [MCSN, MHNG].

D i s c u s s i o n . - All female castes of *pilosus* are very distinctive within the *fiebrigi* clade for their dense, long, flexuous hairs.

The soldiers of *pilosus* show a great variation range in both width and shape of the floor of the disc.

The Argentinean gyne described by SANTSCHI (1921 b) as *pilosus* belongs to *lanuginosus*.

A second Argentinean gyne described by KEMPF (1958 a) as *pilosus* was not available for the present study but is likely to be a true *pilosus* since its short description fits undoubted Brazilian *pilosus* gynes we have been able to see. The gynes of *pilosus* and *lanuginosus* are very similar each other but they can be distinguished at glance (among other characters) by the pilosity denser in *pilosus* than in *lanuginosus*.

D i s t r i b u t i o n : Brazil, Argentina?, Paraguay.

Cephalotes lanuginosus (SANTSCHI) bona species and new combination

Figs. 306, 307, 308

Cryptocerus lanuginosus SANTSCHI, 1919: 46. Worker. Original description. Type locality: Alta Gracia (Córdoba, Argentina). Type material: 2 syntype workers labelled "*Cryptocerus lanuginosus*, type, Sant., Córdoba, Alta Gracia, Bruch leg.", in NHMB, examined. Synonymy with *liogaster* by KEMPF, 1958 a: 25. N e w s y n o n y m.

Cryptocerus lobigaster SANTSCHI, 1919: 47, fig. 4. Worker. Original description. Type locality: Cabana (Córdoba, Brazil). Type material: holotype worker (unique) labelled "*Cryptocerus lobigaster*, type, Sant., Argentine, Cabana, (Scott leg)", in NHMB, examined. Synonymy with *liogaster* by KEMPF, 1958 a: 25. N e w s y n o n y m.

Cryptocerus pilosus EMERY, SANTSCHI, 1921 b: 127. Gyne. Misidentification.

D i a g n o s i s . - A member of the *fiebrigi* clade differing from its sister species, *liogaster*, in the worker, soldier and gyne by the larger and more protruding eyes, and by the subopaque gaster.

W o r k e r (Fig. 306). - Head slightly broader than long. Vertexal angles subround, with slightly crenulate border and with a median pair of denticles. Vertexal margin concave. Frontal carinae slightly upturned over the eyes. Compound eyes large and strongly protruding. Mandibles superficially carinate laterally.

Mesosoma gently convex in side view. Scapular angles reduced but visible in dorsal view. Pronotum with a lateral lamella bearing three pairs of teeth of variable size, the first pair large and pointed, the second and third ones small, more pointed in small workers and simply angulate in large workers. Sides of mesonotum unarmed, rarely with a minute denticle. Promesonotal suture poorly impressed. Propodeal suture superficially impressed. Propodeum with differentiate basal and declivous faces; sides of the basal face with a denticle followed by a tooth, sometimes the denticles simply angulate or absent; sides of the declivous face of the propodeum unarmed, or with two pairs of small denticles.

Petiole with truncate and deeply concave anterior face, and bearing or not a pair of lateral denticles. Petiolar spines arising from the anterior face of the petiole, pointed and curved backwards. Postpetiole as broad as the petiole; its lateral expansions broad, developed anteriorly, curved and pointed backwards.

Gaster suboval, with a pair of broad, anterolateral lobes.

Mid and hind femora not angulate; mid and hind basitarsi flat and with subparallel sides.

Fig. 306. *Cephalotes lanuginosus* (SANTSCHI). Worker from Joaquin V. González (Chaco Occidental), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

Sculpture. Body slightly shining, minutely reticulate-punctate, the reticulation very superficial or absent on the frontal carinae, on the anterior fourth of the first gastral tergite, on the sides of the corresponding sternite, and on the legs. Remaining part of the first gastral sternite shining. Head, mesosoma, pedicel foveolate, the foveae larger, sparser and more regular on the frons, very irregular on the ventral part of the head and on the pedicel. Frontal carinae, ventral part of the head, pleurae and anterior half of the first gastral tergite with additional, thin rugosities, more longitudinally parallel on the frontal carinae, on the sides of the head, on the propleurae and on the anterior half of the first gastral tergite, less regular on the meso- and metapleurae and concentric behind the mouth and in front of the postoccipital bridge. Distal part of the outer face of the femora, and tibiae with superficial, irregular foveae.

Pilosity. Body with four types of hairs: (1) appressed and originating from part of the foveae, of size proportional to the one of the fovea from which they originate; similar hairs of variable size on the body parts without foveae; (2) pointed, long, flexuous, originating either from the undifferentiated integument or from the remaining foveae not bearing type (1) hairs; (3) short and truncate on the two last funicular joints and on the tarsomeres; (4) longer than type (3) and pointed, on the remaining funicular joints and on the mandibles.

Colour. Black. Frontal carinae yellow-orange and semitransparent. Tarsomeres light brown.

Measurements (in mm) and indices: TL 4.32–5.00; HL 1.02–1.16; HW 1.08–1.28; EL 0.30–0.32; PW 0.93–1.16; PeW 0.50–0.64; PpW 0.51–0.65; HBaL 0.41–0.51; HBaW 0.10–0.13; CI 105.9–112.3; PI 110.3–116.1; PPeI 180.0–200.0; PPpI 178.5–186.2; HBaI 22.94–25.5.

S o l d i e r (Fig. 307). - Head as broad as long, with complete disc. Floor of the disc convex posteriorly and concave anteriorly. Frontal carinae and borders of the disc strongly crenulate and raised only anteriorly. Sides of the disc subparallel, converging backwards, not hiding the eyes and connected by the convex posterior border of the disc. Vertexal angles broad, convex, converging towards the vertex and with strongly crenulate border. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a longitudinal, denticulate carina just in front of the eyes.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of pointed teeth. Pronotal sides gently convex with or without a crenulate border on the anterior half only. Pronotal carina generally well marked (less so among small specimens), strongly crenulate and medially interrupted by a sulcus. Promesonotal suture deep and less impressed medially. Sides of the mesonotum with a small, broad, round expansion. Propodeal suture impressed. Propodeum with well differentiate basal and declivous faces. Sides of the basal face with a small pair of short, broad, subround or truncate teeth and with a pair of large, stout teeth curved upwards. Declivous face medially concave, its sides converging posteriorly.

Petiole with the anterior face oblique and deeply concave medially, its sides with a pair of pointed spines curved backwards. Postpetiole convex. Postpetiolar sides with a pair of thick, round expansions arising from the anterior border, directed anterolaterally and pointed backwards.

Gaster oval and with a pair of anterolateral lobes.

Mid and hind femora without angles or denticles. Hind basitarsi with subparallel sides.

Sculpture. Head, mesosoma and pedicel, outer face of the femora and of the tibiae superficially shining, minutely reticulate-punctate and foveolate; the foveae more regular on the head dorsum, sparser on the frontal carinae, smaller on the pedicel. Pleurae with rugosities superimposed to the reticulation, the rugosities longitudinal on the propleurae, irregular on the meso- and lower metapleurae and oblique on the upper metapleurae. Gaster reticulate, the reticulation less impressed on the posterior half of the first gastral sternite. Anterior fourth of the first gastral tergite with additional, small, superficial foveae and with few longitudinal rugosities. Distal part of the outer face of the femora, and tibiae with superficial, irregular, small foveae.

Pilosity. As in the worker.

Colour. Black. Head dorsum and pronotal sides orange to light brown. First gastral tergite with two pairs of orange spots, the first pair behind the lobes and the second one close to the posterior border. Few specimens with the whole pronotum, part of the mesonotum, the

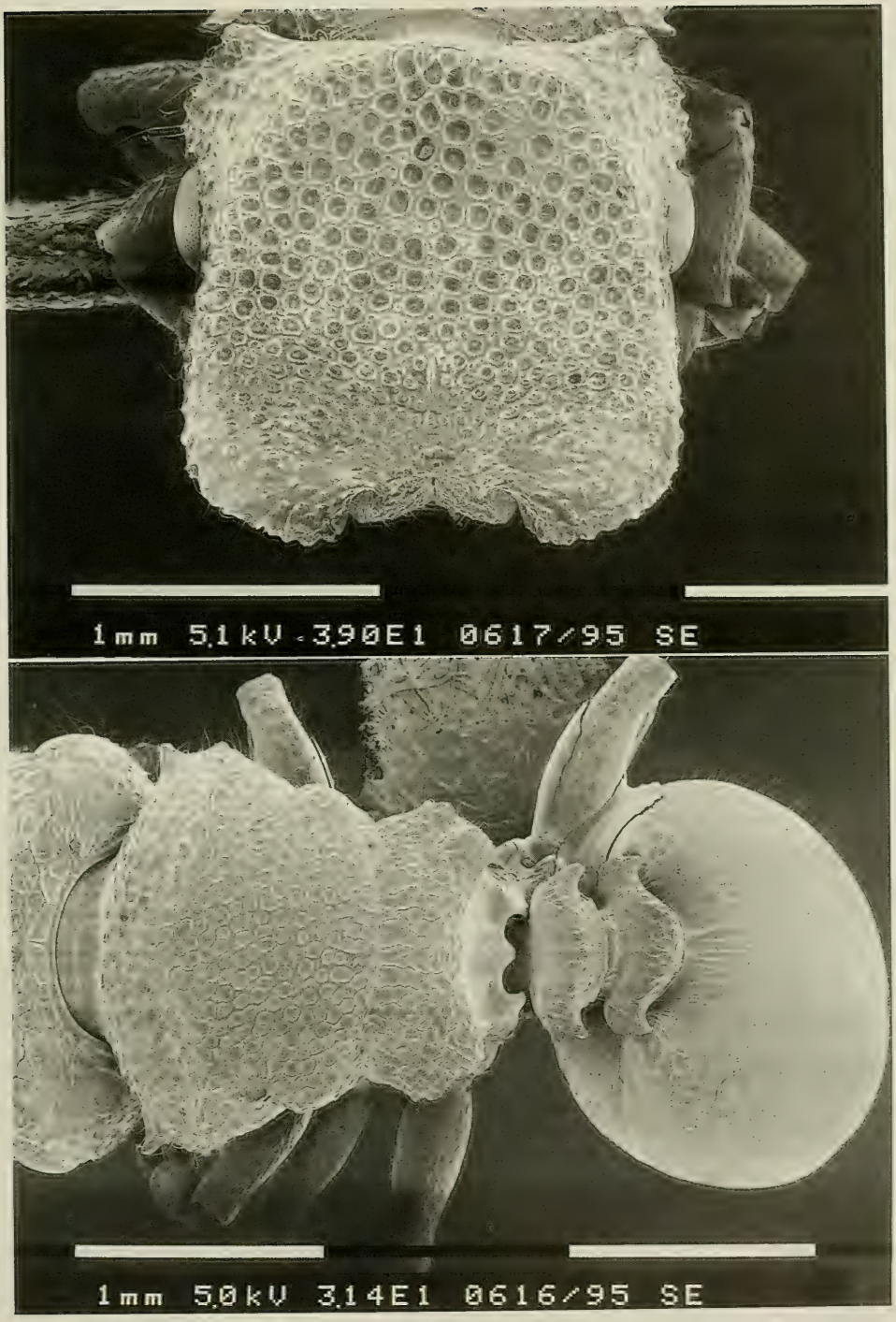


Fig. 307. *Cephalotes lanuginosus* (SANTSCHI). Soldier from Joaquin V. González (Chaco Occidental), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

propodeal sides, and the outer ace of the tibiae orange. Some specimens without gastral spots.

Measurements (in mm) and indices: TL 6.56–8.02; HL 1.72–1.96; HW 1.68–1.96; EL 0.36–0.40; PW 1.60–1.92; PeW 0.70–0.84; PpW 0.73–0.84; HBaL 0.45–0.51; HBaW 0.14–0.16; CI 97.7–102.3; PI 102.1–105.0; PPeI 225.3–240.0; PPpI 219.2–228.6; HBaI 31.1–31.4.

Gyne. - Head of variable width, slightly narrower or broader than long, with a complete disc. Floor of the disc convex posteriorly and gently concave anteriorly. Frontal carinae and borders of the disc strongly crenulate and raised anteriorly only. Sides of the disc converging backwards, not hiding the protruding eyes and connected by a convex or truncate border; small gynes have the posterior sides of the disc with less marked border. Vertexal angles convex, with a median pair of denticles and with crenulate border. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a longitudinal carina bearing a tooth in front of the eyes; the tooth may be preceded by a crenulation among small specimens.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of small denticles. Pronotal sides straight and sometimes weakly marginate. Pronotal carina well marked and strongly crenulate in large specimens; small specimens have the pronotal carina less marked on the sides. Mesonotum and scutellum flat. Propodeum with well differentiate basal and declivous faces. Sides of the basal face with a small pair of short, obtuse denticles and with a pair of large teeth pointing laterally. Declivous face medially concave; its sides converging posteriorly and superficially carinate laterally.

Petiole with the anterior face oblique and deeply concave medially; its sides with a pair of small, pointed denticles curved backwards. Postpetiole convex. Postpetiolar sides with a pair of variably developed round expansions arising from the anterior border and directed backwards.

Gaster with a pair of protruding anterolateral lobes.

Mid and hind femora without angles or denticles. Hind basitarsi with subparallel sides.

Sculpture. As in the soldier except for the foveae, less impressed on the mesonotum and on the scutellum.

Pilosity. As in the worker and soldier.

Colour. As in the soldier.

Measurements (in mm) and indices: TL 8.78–9.32; HL 1.72–1.74; HW 1.68–1.78; EL 0.40; PW 1.60–1.76; PeW 0.64–0.73; PpW 0.74–0.87; HBaL 0.57–0.60; HBaW 0.16; CI 97.7–102.3; PI 101.1–105.0; PPeI 241.1–250.0; PPpI 202.3–216.2; HBaI 26.7–28.1.

Male (previously undescribed). - Very similar to the male of *pilosus* but differing from it in the details listed below:

Eyes larger. Scutellum broader and less convex dorsally. Anterior face of the petiole less concave. Petiole and postpetiole broader.

Genitalia and subgenital plate as in Fig. 308.

Sculpture. First gastral tergite more shining. Body rugosities more regular, parallel; thicker on the propodeum and on the pedicel.

Pilosity. Flexuous hairs less dense.

Colour. Black. Distal third of the femora, tibiae and tarsi dark yellow.

Measurements (in mm) and indices: TL 5.88–6.56; HL 0.90–0.92; HW 1.16; EL 0.48; PW 1.04–1.10; PeW 0.60; PpW 0.63; HBaL 0.52–0.55; HBaW 0.12–0.13; CI 126.1–128.9; PI 105.4–111.5; PPeI 173.3–183.3; PPpI 165.1–174.6; HBaI 23.1–23.6.

Material examined. - **Argentina**: no further locality, 1 worker (without head) [MCZC]; no further locality, 8 workers, 15 soldiers, 6 gynes, 8 males, [ZSMC]. Salta: Chaco Occidental, Los Colorados, 50 km NE of Joaquin V. Gonzáles, 04.III.1992, 2 workers, 2 soldiers, B. Bestelmeyer [LACM]. Santiago del Estero: Río Dulce, 1 gyne, E. R. Wagner [NHMB]; nr. Santiago del Estero, 1 soldier, C. Bruch [MZSP]. Tucumán: La Soledad, Cañete, Dep. Cruz Alta, 27.I.1966, 2 workers E. H. Bucher [MCZC, MZSP]. Córdoba: Alta Gracia, 2 workers (syntypes), Bruch [NHMB];

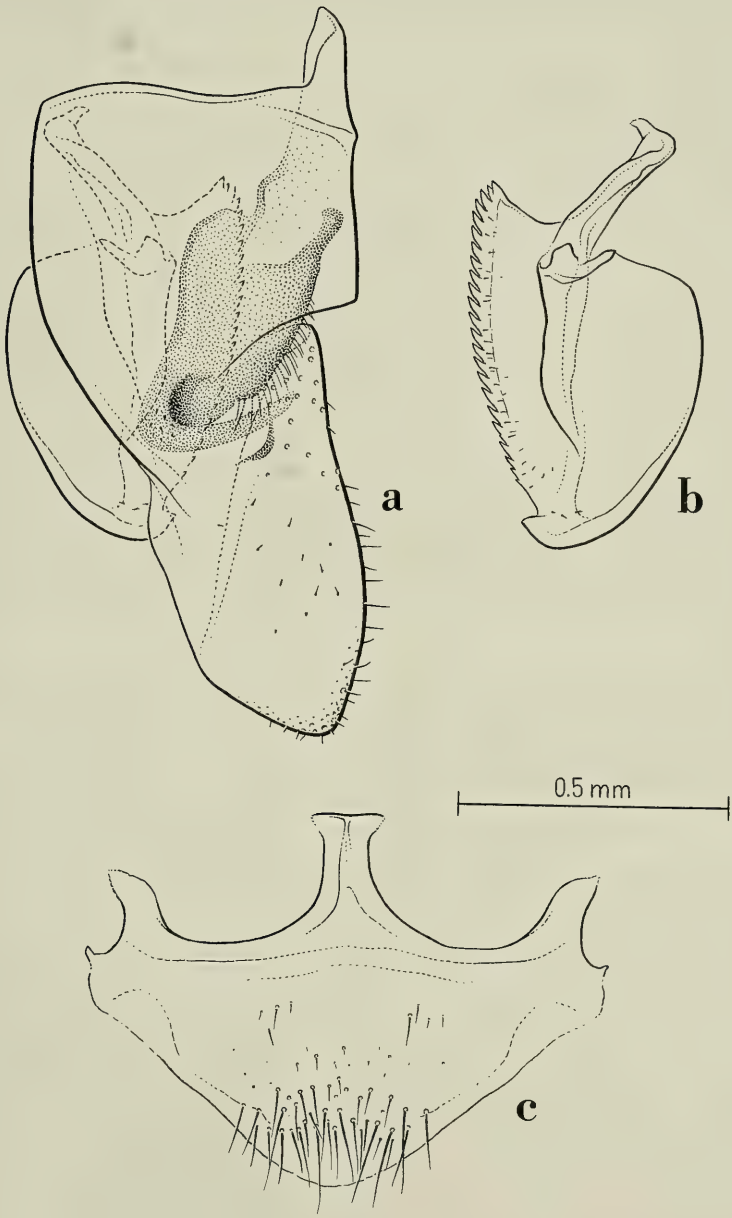


Fig. 308. *Cephalotes lanuginosus* (SANTSCHI). Male from Argentina (no further locality). Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

same locality, 1 soldier, BRUCH [NHMB] (identified as *ellenriederi* var. *jocans* by Santschi); Cabana, 1 worker (holotype of *lobigaster*), SCOTT [NHMB].

D i s c u s s i o n . - *C. lanuginosus* had been synonymised with *liogaster* by KEMPF (1958 a). The two species are very similar and both show great morphological and sculptural variation. The main differences between *lanuginosus* and *liogaster* are given in the diagnosis; other minor but constant differences worth to be mentioned are: all three female castes have (1) the ventral process of the petiole with a small, round denticle in *lanuginosus* vs. broad and truncate in *liogaster*; and (2) the mesonotal expansions extremely small (sometimes absent in the workers) in *lanuginosus* vs. well developed in *liogaster*. In addition to that, large soldiers and large gynes of *lanuginosus* have a well developed pronotal crest, much higher than the one of *liogaster* soldiers and gynes independently of their size.

The gyne described by SANTSCHI (1921) as *pilosus* should be referred to *lanuginosus* although it is slightly larger than the other gynes and the sides of the disc are strongly narrowed backwards and well marked postero-laterally.

D i s t r i b u t i o n : Argentina.

Cephalotes liogaster (SANTSCHI) new combination
Fig. 309

Cryptocerus liogaster SANTSCHI, 1916: 381, fig. without number. Worker. Original description. Type locality: Estación Sosa (Entre Ríos, Argentina). Type material: 3 syntype workers in NHMB (examined).

Cryptocerus lobigaster var. *fides* SANTSCHI, 1925: 162. Worker, soldier and gyne. Original description. Type locality: Fives Lille (Santa Fé, Argentina). Type material: 4 workers, 4 soldiers and 1 gyne, all syntypes in NHMB (examined); 1 worker labelled as paratype in MZSP, examined; additional syntype material presumably in the Museo Nacional de Historia Natural, Buenos Aires (not seen). Synonymy by KEMPF, 1958 a: 25.

Paracryptocerus liogaster (SANTSCHI), KEMPF, 1958 a: 25, figs. 16, 18, 21, 28. Worker, soldier and gyne. First combination in *Paracryptocerus*.

Zacryptocerus liogaster (SANTSCHI), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *fiebrigi* clade differing from its sister species *lanuginosus* in the worker, soldier and gyne by the smaller and less protruding eyes and by the more shining gaster.

W o r k e r (Fig. 309) (description of KEMPF, 1958 a, list of differential characters with *pilosus* q. v.). - "Length 4.4–5.2 mm. Sculpture of first gastral tergite superficial to obsolete; integument always shining, often quite smooth. 2. Thoracic and peduncular teeth or spines usually more acute, peduncular spines more reflexed caudad, especially in shinier specimens. 3. Postpetiole middorsally often, not always, acuminate as in *fiebrigi*. 4. First gastral tergite in general longer, with less convex sides and more pronounced anterolateral lobes. 5. Standing hair slightly longer, less crowded; scalelike, appressed hair more delicate and shorter, masking to a lesser degree the integument."

Measurements (in mm) and indices: TL 4.32–5.16; HL 0.98–1.16; HW 1.06–1.26; EL 0.26–0.30; PW 0.92–1.12; PeW 0.51–0.60; PpW 0.54–0.59; HBaL 0.35–0.47; HBaW 0.09–0.12; CI 105.3–108.6; PI 107.1–116.7; PPeI 180.4–211.3; PPpI 170.4–196.5; HBaI 25.5–26.7.

S o l d i e r (description of KEMPF, 1958 a, list of differential characters with *pilosus* q. v.). - "Length 6.0–7.8 mm. 1. Head disc, shoulders, tips of posterior epinotal teeth, extensor face of tibiae yellowish-brown. Frequently, especially in larger, full-grown soldiers, the light color

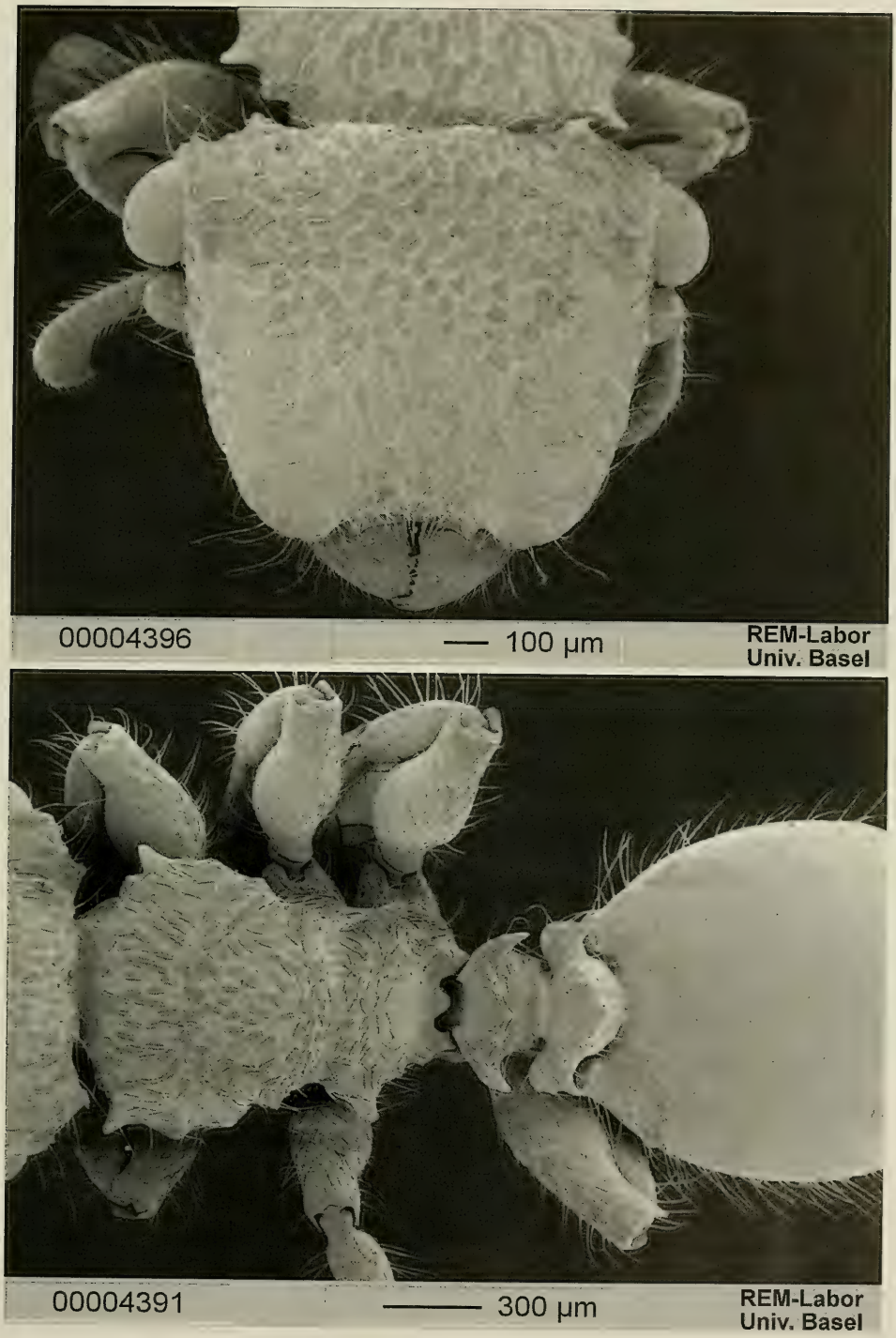


Fig. 309. *Cephalotes liogaster* (SANTSCHI). Worker from Fives Lilles (Santa Fé), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

extends over the entire promesonotum and sometimes also the epinotum. In this case, the first gastral tergite is marked by four yellowish spots, variable in size, one at each corner. 2. Posterior epinotal teeth shorter, their tips never raised, but pointing obliquely caudad. 3. Peduncular spines more reflexed at apex. 4. Gaster more elongate, finely and densely punctate, but always shining."

Measurements (in mm) and indices: TL 7.68–7.80; HL 1.68–1.76; HW 1.76–1.92; EL 0.33–0.34; PW 1.68–1.82; PeW 0.75–0.8; PpW 0.71–0.84; HBaL 0.44–0.52; HBaW 0.14–0.16; CI 104.8–109.1; PI 104.8–105.5; PPeI 224.0–227.5; PPpI 216.7–236.6; HBaI 30.8–31.8.

G y n e (description of KEMPF, 1958 a, list of differential characters with *pilosus* q. v.). - "Length 7.8–9.1 mm. 1. Head disc predominantly yellowish-brown. The same color prevails on the extensor face of the tibiae, the pronotum and also on the scutum, with the exception of two lateral and often one median black streaks on the latter. First gastral tergite with the customary four large testaceous spots, one at each corner. 2. Peduncular spines more recurved, the postpetiole narrower and longer, the anterior border of the gaster more deeply excised. 3. First gastral tergite finely but densely sculptured, the integument nevertheless quite shining.

Females of this species sometimes exhibit a striking variability in coloration and development of head disc, a phenomenon commonly observed only in the soldier caste. Two specimens, measuring 7.8 and 8.0 mm, have the head disc indistinctly marginate posterolaterally, in front of the occipital lobes. One specimen is rather dark, the light color being restricted to the border of the head disc, the tips of the scapular angles, the tibiae and the four spots on the gaster. A single winged specimen has the wings infuscated with dark brown veins. The fore wing measures 7.1 mm, and extends well beyond the posterior end of the gaster, when folded over the back."

Measurements (in mm) and indices: TL 8.92–9.56; HL 1.64–1.76; HW 1.64–1.80; EL 0.36–0.39; PW 1.68–1.72; PeW 0.73–0.75; PpW 0.84–0.88; HBaL 0.58–0.64; HBaW 0.16–0.17; CI 100.0–102.3; PI 97.6–104.6; PPeI 229.3–230.1; PPpI 195.4–200.0; HBaI 25.0–29.3.

M a t e r i a l e x a m i n e d . - **Argentina**: no further locality, 2 workers [MCZC]. C a t a m a r c a : La Cienaga (Belén), 1926, 1 worker, 1 soldier, 1 gyne, WEISER & WOLTERS [MZSP]. L a R i o j a : Rt. 20, km 915 E of Chepes, 19.XII.1967, in *Prosopis nigra*, 1 worker, C. R. WARD [USNM]. S a n t a F é : Fives Lille, 7 workers, 4 soldiers, 1 gyne (all syntypes of var. *fides*), C. BRUCH [MZSP, NHMB]; Rosário, 1 worker, 1 soldier, W. M. DAVIS [MCZC]. E n t r e R í o s : Estación Sosa, 3 workers (syntypes of *liogaster*), MAC DONAGH [NHMB].

D i s c u s s i o n . - We can only confirm KEMPF's (1958 a) synonymy of *lobigaster* var. *fides* with *liogaster*. On the other hand, other synonyms of *liogaster* proposed in the same paper (*lanuginosus* and *lobigaster*) have been already treated as a separate species (*lanuginosus*) by us or as a synonym of *lanuginosus* (*lobigaster*). *Lanuginosus* is actually the species closest to *liogaster* but the size of the eyes and the sculpture of the gaster appear to discriminate between all the specimens we refer to these two species (23 and 27 respectively).

D i s t r i b u t i o n : Argentina.

Cephalotes quadratus (MAYR) new combination
Fig. 310

Cryptocerus quadratus MAYR, 1868: 175. Soldier. Original description. Type locality: Estancia Salvador near San Luís (San Luís, Argentina). Type material: Holotype soldier labelled "Salvador, Strobel. 9., Collect. G. Mayr, *quadratus*, G. Mayr Type" in NHMW (KEMPF, 1958 a: 34), examined.

Cryptocerus convexus SANTSCHI, 1916: 382, fig. Worker. Original description. Type locality: Estación Sosa (Entre Rios, Argentina). Type material: 3 syntype workers labelled

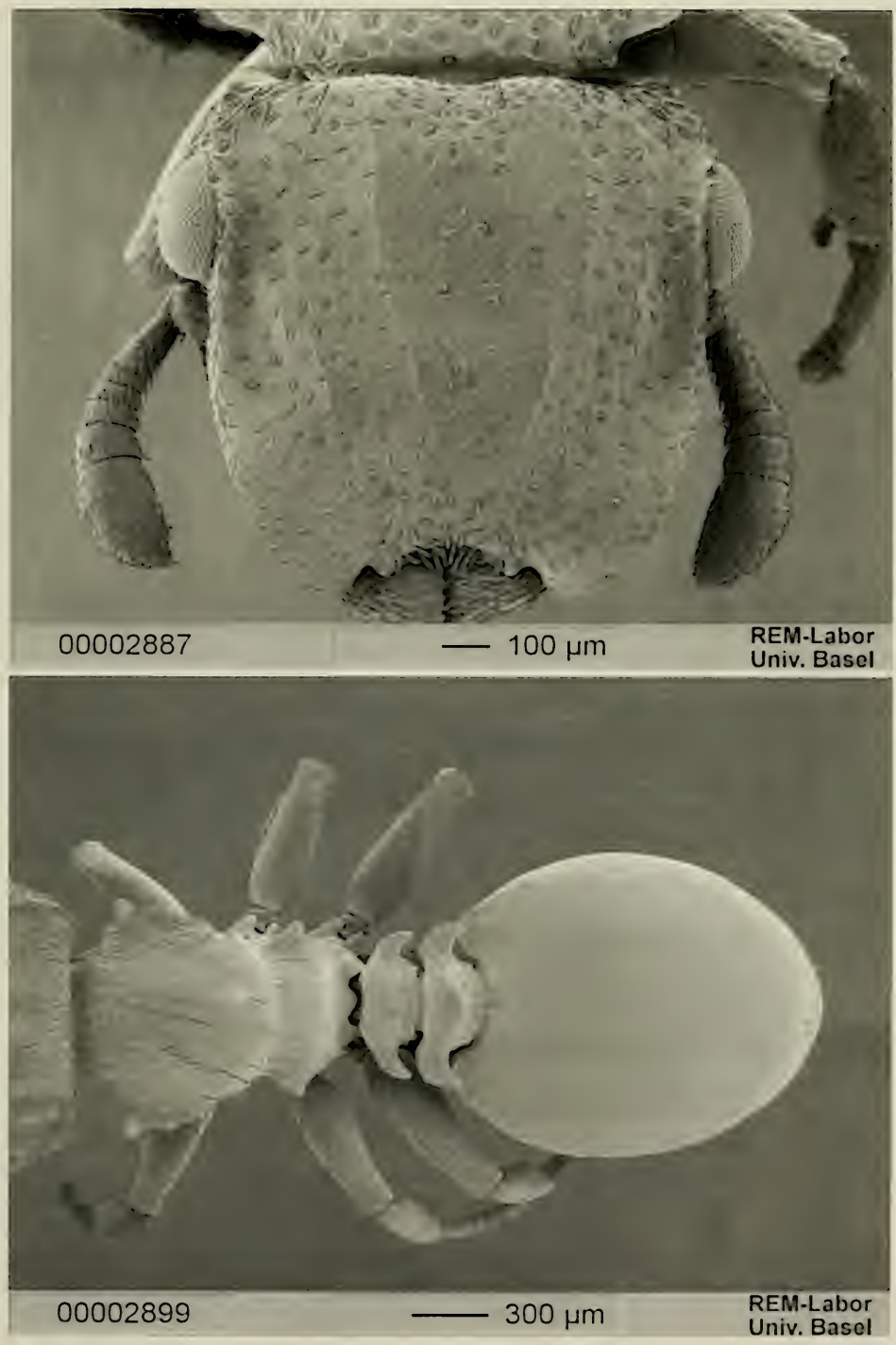


Fig. 310. *Cephalotes quadratus* (MAYR). Worker from Estación Sosa (Entre Rios), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

"Argentine, Entre Rios, Estación Sosa, Mac Donagh", in NHMB; 1 worker (probably syntype) labelled "Est. Sosa, *Cryptocerus convexus*", in MZSP, all examined. Synonymy by KEMPF, 1958 a: 33.

Paracryptocerus quadratus (MAYR), KEMPF, 1958 a: 33, figs. 10 and 26 (nec fig. 4 and 22 = worker of *guayaki*). Partim. Soldier and? gyne, nec worker. First combination in *Paracryptocerus*.

Zacryptocerus quadratus (MAYR), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *fiebrigi* clade differing from the two species of its sister subclade, *guayaki* and *fiebrigi*, in the worker and soldier by the absence of erect hairs on the head, mesosoma and pedicel.

W o r k e r (Fig. 310). - Head broader than long and strongly convex dorsally. Vertexal angles round and with an obtuse denticle medially. Vertexal margin narrowly concave. Frontal carinae concave in front of the eyes and sinuous over the eyes. Mandibles laterally carinate.

Mesosoma strongly convex in side view. Scapular angles visible in dorsal view. Pronotum with a narrow lateral lamella bearing three pairs of irregular teeth, the first pair larger and obtuse and the second and third ones round. Sides of mesonotum with a pair of small denticles. Promesonotal suture poorly impressed. Propodeal suture impressed. Propodeum with differentiate basal and declivous faces and with the sides narrowing backwards; sides of the basal face of the propodeum with two pairs of teeth, the first pair simply angulate and the second one larger and pointed; sides of the declivous face of the propodeum unarmed, or with one or two small pairs of denticles.

Petiole anteriorly truncate; its anterior border weakly concave medially. Petiolar dorsum with a transversal carina separating its anterior face from the posterior one. Petiolar spines well developed arising from the anterior face of the petiole, pointed and strongly curved backwards. Postpetiole slightly broader than the petiole; its lateral expansions broad, spiniform, developed and directed anteriorly, strongly curved and pointed backwards.

Gaster suboval, with a pair of broad, anterolateral lobes.

Mid and hind femora not angulate; mid and hind basitarsi flat and with subparallel sides.

Sculpture. Body slightly shining, minutely and superficially reticulate-punctate. Head, mesosoma, pedicel and outer face of the femora and tibiae superficially foveolate, the foveae more impressed close to the vertexal margin and on the pronotum, irregular on the lower pleurae, on the pedicel and on the outer face of the femora and tibiae, rare or absent on the frontal carinae, on the declivous face of the propodeum, on the propleurae and on the upper meso- and metapleurae. Propleurae with additional thin, longitudinal rugosities.

Pilosity. Body with four types of hairs: (1) appressed and generally originating from each fovea; similar hairs on some body parts without foveae; (2) subclavate and rare on the border of the frontal carinae and on the legs; (3) subtruncate and rare on the dorsum of the first gastral tergite, sparse on the corresponding sternite; similar hairs but longer on the posterior borders of the gastral segments; (4) long, pointed and rare on the posterior borders of the sternites.

Colour. Brown. Frontal carinae dark yellow-orange.

Measurements (in mm) and indices: TL 4.26–4.56; HL 1.00–1.08; HW 1.06–1.16; EL 0.30–0.36; PW 0.92–1.00; PeW 0.58–0.62; PpW 0.60–0.65; HBaL 0.36–0.39; HBaW 0.07–0.08; CI 106.0–107.4; PI 115.2–116.0; PPeI 158.6–161.3; PPpI 153.3–153.8; HBaI 19.4–20.5.

S o l d i e r (description of KEMPF, 1958 a). - "Total length about 6.4 mm (not accurately measured when type was available); maximum length of head 1.62 mm; of thorax 1.80 mm. Fuscous-brown to black; anterolateral portions of head disc and shoulders reddish-brown; antennae and legs rufo-testaceous. First gastral tergite quadrimaculate, the spots being yellow, rather small, the posterior pair at some distance from the apical border. Integument slightly shining.

Head subquadrate but slightly longer than broad (67:65), surmounted by an incompletely marginate disc, i. e. anteriorly, anterolaterally and posteriorly the disc is sharply marginate,

forming a slightly raised crest, which is distinctly crenulate anterolaterally. Postero-laterally, above eyes and the occipital lobes, the border is obsolete and the upper face is continuous with the sides of the head. In profile, the head is strongly convex above. Transversely, the disc is concave in front, gently convex behind. Clypeal sutures vestigial. Eyes situated behind and slightly above the antennal scrobe. Penultimate funicular segment nearly twice as long as the preceding segment. Occipital angles subrectangular and slightly crested. Head disc, occiput and sides coarsely reticulate-rugose and foveolate, with suberect, slightly curved and spatulate hair arising from each pit.

Thorax longer than broad (74:59). Shoulders distinctly dentate. Promesonotum conspicuously convex, as seen in profile. Transverse pronotal carina distinct at the sides, obsolete in the middle. Lateral border of dorsal face of pronotum distinctly marginate in front of the transverse carina, immarginate and rounded behind. Promesonotal suture vestigial at the sides, absent in the middle. Lateral borders of mesonotum forming a rounded, projecting lobe on each side. Mesoepinotal suture impressed, rather deeply laterally, more superficially in the middle. Sides of basal face of epinotum immarginate, with a projecting tubercular swelling. The posterior corner with an obtuse, stout, tubercular tooth. Posterior border, between the teeth, gently emarginate, not forming a marginate edge between the basal face and the declivity, which forms about a right angle with the former. Sculpture of dorsum of thorax almost as on head disc, but the pits are sparser, and the hairs arising from them are decumbent, silvery. Sides of thorax with still more scattered foveolae and the intervening spaces reticulate-rugose, the intervals between the rugosities being finely punctate. Extensor face of tibiae rugulose. Femora fusiform, tibiae and tarsi subcylindrical.

Petiole, in dorsal view, with evenly curved anterior border, which continues laterally as the anterior border of the recurved spines. In the middle, the body of the petiole has a gently impressed longitudinal furrow, flanked on each side by a vestigial swelling. From spine to spine, across the body of the segment extends a bluntly edged, sinuate, transverse carina. Postpetiole slightly broader than petiole, its lateral spines in the form of a pigeon wing, pointing obliquely cephalad at base, strongly recurved caudad. Transverse, blunt carina present, forming a feeble tooth middorsally. Both peduncular segments irregularly rugose, with longer, appressed scalelike hair.

Gaster deeply excised anteriorly, between the projecting, more or less rounded, anterolateral lobes, the border of which is neither crested nor lamellate. Gaster elongate, almost twice as long as broad, its sides subparallel. First tergite finely and densely punctate, with long, appressed, scalelike hair at base, the rest being subglabrous. The apical end of the following tergites and the sternites bear short, sparse, suberect hairs."

Measurements (in mm) and indices: TL 6.48; HL 1.48; HW 1.48; EL 0.34; PW 1.40; PeW 0.72; PpW 0.76; HBaL 0.39; HBaW 0.10; CI 100.0; PI 105.7; PPeI 194.4; PPpI 184.2; HBaI 25.6.

Material examined. - **Argentina**: San Luís: Estancia Salvador nr. San Luís, P. DE STROBEL, 1 soldier [NHMW]. Entre Ríos: Estación Sosa, 4 workers (syntypes), MAC DONAGH [NHMB, MZSP].

Discussion. - EMERY (1896) described all castes of *quadratus* (MAYR) on a series of specimens from Paraguay. He correctly noted that the Paraguayan soldiers were much smaller than the *quadratus* type. Our examination of the specimens mentioned by EMERY (1896) convinced us that they belong to a new species that we shall describe in this paper as *guayaki*. *Convexus* has been considered a junior synonym of *quadratus* by KEMPF (1958 a). This opinion, however, was based upon comparison of a *convexus* syntype with some specimens of *quadratus* identified by EMERY (= *guayaki*). Our examination of all syntypes of *convexus* and of the *quadratus* holotype shows that the former is actually a junior synonym of the latter. KEMPF (1958 a) described for the first time the gyne of *quadratus* on the basis of an Argentinean gyne preserved in Buenos Aires. We requested this specimen in study

and received no reply. The attribution of KEMPF is plausible, but since, under the name *quadratus*, he confused this species with *guayaki*, we do not report the description of this gyne under either of the two species.

Distribution: Argentina.

Cephalotes guayaki DE ANDRADE new species
Figs. 311, 312

Cryptocerus quadratus MAYR, EMERY, 1896: 634, fig. E. Worker, soldier, gyne. Nec MAYR, 1868. Misidentification.

Paracryptocerus quadratus (MAYR), KEMPF, 1958 a: 33, figs. 4 and 22, (nec fig. 10 and 26 = soldier of *quadratus*). Partim. Worker (and gyne?), nec soldier. Misidentification.

Type material: Holotype worker from San Salvador, Paraguay, BOHLS leg. in MCSN; paratypes 13 workers, 6 soldiers, 1 gyne, same data as the holotype in MCSN, 1 worker, same data as the holotype in MHNG.

Derivatio nominis: The Guayakí are one of the Indian tribes of Paraguay.

Diagnosis. - A member of the *fiebrigi* clade differing from its sister species, *fiebrigi*, in the worker, soldier and gyne by the body with sparser erect, truncate hairs.

Worker (Fig. 311). - Differing from *quadratus* in the following details:

Head slightly longer than broad and less convex dorsally. Vertexal angles subtruncate. Frontal carinae concave in front of the eyes and superficially sinuous over the eyes.

Mesosoma less convex in profile. Pronotal lamellae less converging posteriorly. First pair of pronotal spines less protruding. Basal face of the propodeum with two pairs of teeth subequal in size.

Lateral expansions of the postpetiole developed anteriorly and oriented more ventrally.

Sculpture. Head, mesosoma, pedicel, outer face of the femora and tibiae with more impressed foveae. Propleurae with rare, thin, longitudinal rugosities.

Pilosity. Hairs of type (3) of *quadratus* (where they are restricted to the gaster) also present on the dorsum of the head, of the mesosoma, of the pedicel, and denser on the dorsum of the first gastral tergite.

Colour. Black. Legs brown. Frontal carinae light brown.

Measurements (in mm) and indices: TL 3.74–3.88; HL 0.88–0.90; HW 0.85–0.88; EL 0.25–0.26; PW 0.76; PeW 0.47–0.48; PpW 0.50–0.52; HBaL 0.32–0.33; HBaW 0.07–0.08; CI 96.6–97.8; PI 111.8–115.8; PPeI 158.3–161.7; PPpI 146.1–152.0; HBaI 21.8–24.2.

Soldier (Fig. 312). - Head longer than broad, with complete disc. Floor of the disc convex only on the posterior third and gently concave anteriorly. Frontal carinae and borders of the disc crenulate and raised anteriorly. Sides of the disc strongly narrowing backwards, not hiding the eyes and connected by a convex border; posterolateral borders of the disc less marked. Vertexal angles slightly convex and with a median triangular tooth. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a longitudinal, denticulate carina just in front of the eyes.

Mesosoma. Anterior pronotal border gently convex. Humeral angles with a pair of small denticles. Pronotal sides straight. Pronotal carina superficially marked. Promesonotal suture superficially impressed. Sides of the mesonotum with a broad, subround tooth. Propodeal suture impressed. Propodeum with well differentiate basal and declivous faces. Sides of the basal face with one or two small, round denticles followed by a stout tooth gently curved upwards. Declivous face converging posteriorly.

Petiole and postpetiole as in the worker but with the lateral expansions less developed.

Mid and hind femora without angles or denticles. Hind basitarsi with subparallel sides.

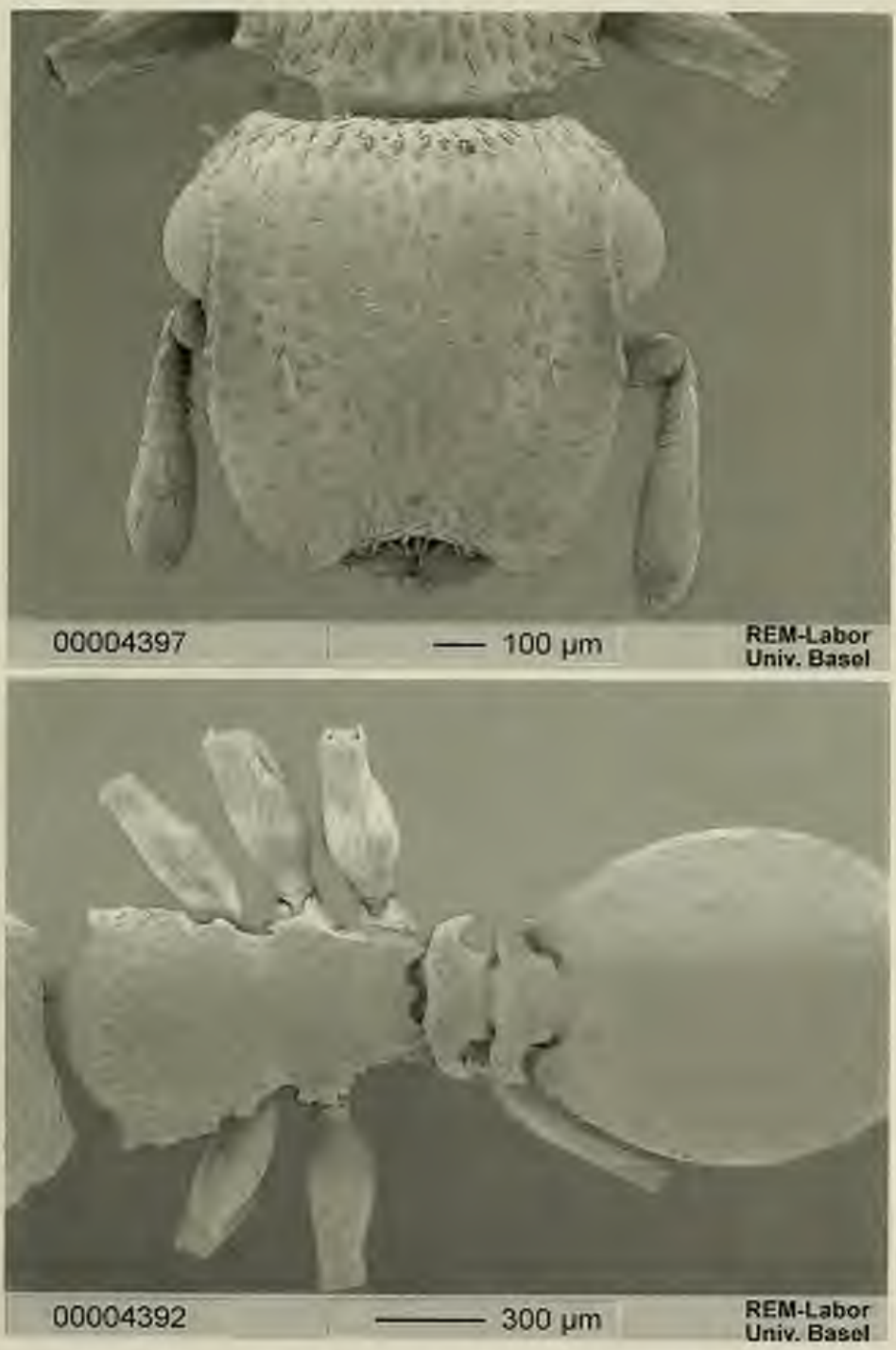


Fig. 311. *Cephalotes guayaki* DE ANDRADE. Worker from San Salvador, Paraguay: head (top) and meso- and metasoma (bottom) in dorsal view.

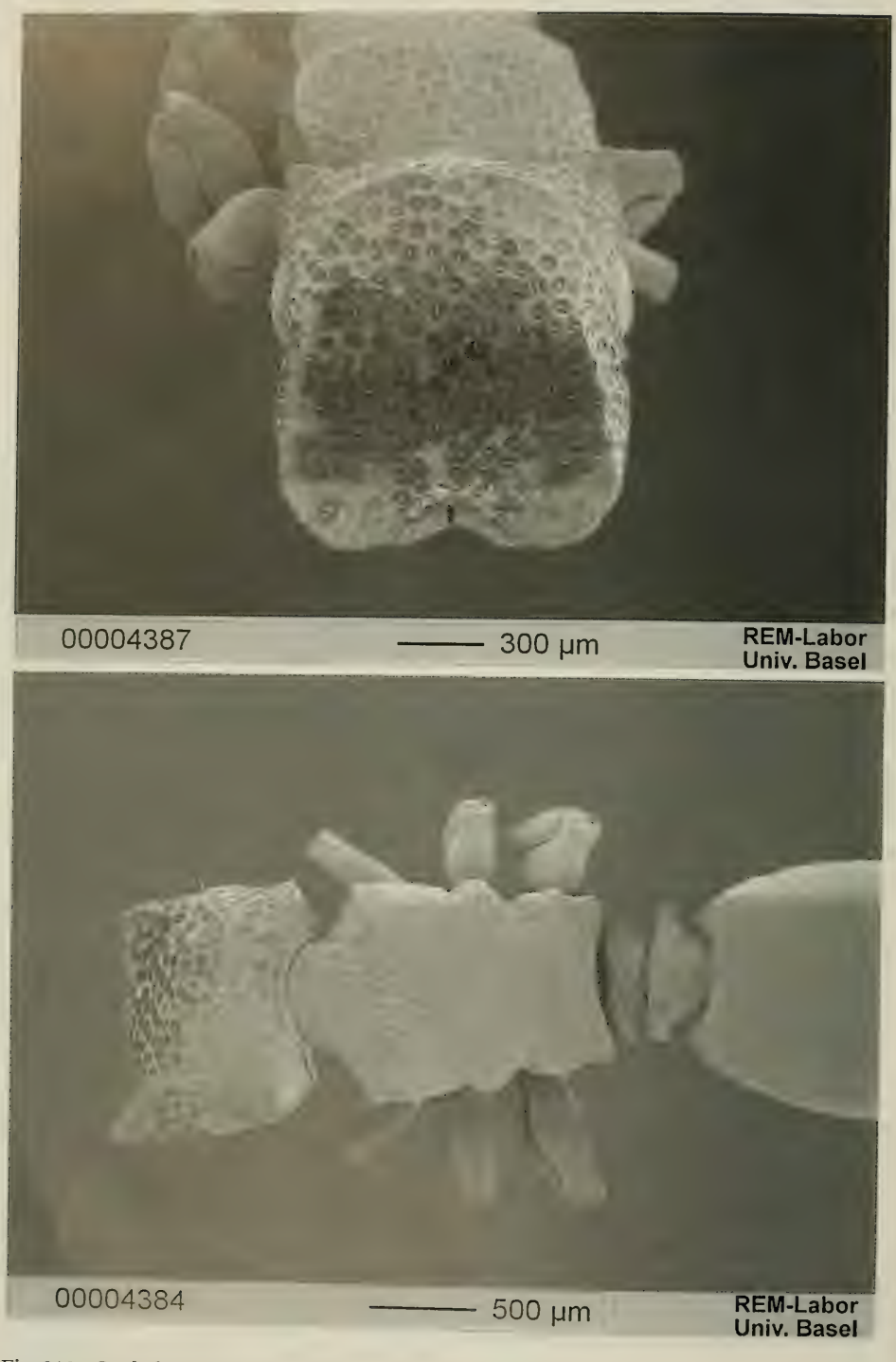


Fig. 312. *Cephalotes guayaki* DE ANDRADE. Soldier from San Salvador, Paraguay: head (top) and meso- and metasoma (bottom) in dorsal view.

Gaster with narrow anterolateral lobes protruding anteriorly.

Sculpture. Head, mesosoma, pedicel, distal part of the outer face of the femora and tibiae minutely reticulate-punctate, superficially shining and foveolate, the foveae contiguous and deeper on the head dorsum and on the pronotum, slightly sparser and shallower on the ventral part of the head and on the mesonotum, oval and very superficial on the basal face of the propodeum, on the pedicel, on the outer face of the femora and on the tibiae, rare on the pleurae. Pro- and lower meso- and metapleurae with additional thin, longitudinal rugosities. Gaster and remaining parts of the legs reticulate, the reticulation more impressed on the first gastral tergite.

Pilosity. Body with three types of hairs: (1) canaliculate, originating from the foveae, subdecumbent on the head dorsum, appressed on the rest of the body, slightly shorter and thinner on the body parts without foveae; (2) subclavate and rare on the posterolateral border of the frontal carinae; (3) subtruncate and sparse on the mesosoma, on the pedicel, on the gaster and on the legs.

Colour. Black. Anterior half of the frontal carinae, pronotal sides and legs dark orange-ferruginous. First gastral tergite with two pairs of yellow spots, the first pair close to the lobes and the second one close to the posterior border.

Measurements (in mm) and indices: TL 4.76–5.56; HL 1.24; HW 1.12–1.16; EL 0.30–0.31; PW 1.04; PeW 0.55–0.59; PpW 0.57–0.64; HBaL 0.34; HBaW 0.10; CI 90.3–93.5; PI 107.7–111.5; PPeI 176.3–189.1; PPpI 162.5–182.4; HBaI 29.4.

Gyne. - Differing from the soldier in the following details:

Head slightly longer than broad. Vertexal angles simply angulate medially. Humeral angles only angulate. Pronotal sides straight. Mesonotum and scutellum flat. Sides of the basal face of the propodeum with a small pair of short, round denticles and with a pair of small, stout teeth, slightly diverging. Petiolar sides with a pair of small, pointed denticles. Postpetiolar spines smaller. Gaster longer and with more protruding lobes.

Sculpture. Foveae sparser on the mesonotum and denser on the upper mesopleurae. Pleurae with rugosities present only on the lower propleurae. The rest as in the soldier.

Pilosity. Mesosoma, pedicel, gaster and legs with hairs of type (3) denser.

Colour. As in the soldier except for the frontal carinae dark orange-ferruginous.

Measurements (in mm) and indices: TL 6.12; HL 1.20; HW 1.08; EL 0.31; PW 1.02; PeW 0.52; PpW 0.57; HBaW 0.10; CI 90.0; PI 105.8; PPeI 196.1; PPpI 170.0.

Material examined. - **Paraguay**: San Salvador, 15 workers, 6 soldiers, 1 gyne, BOHLS [MCSN, MHNG].

Brazil: Mato Grosso do Sul: Porto Murtinho, IV.1959, 1 gyne, B. KELBER [MZSP].

Discussion. - The gyne from Porto Murtinho is as small as and identical to the Paraguayan one doubtfully attributed to *quadratus* by EMERY (1896) and belonging to the same series on which we based the first description of *guayaki*. The size of the Paraguayan soldiers (TL 4.76–5.56) we refer to *guayaki* is much less than that of the true *quadratus* soldier (TL 6.48). The size of the Brazilian gyne we refer to *guayaki* (TL 6.12 mm) is also smaller than that of the sole *quadratus* soldier known to date. The body size, together with the pilosity, seem to represent the main characters useful to separate *guayaki* from *quadratus*.

Distribution: Brazil (Mato Grosso do Sul), Paraguay.

Cephalotes fiebrigi (FOREL) new combination

Figs. 313, 314, 315, 316, 317

Cryptocerus pilosus fiebrigi FOREL, 1906: 235. Worker and soldier. Original description. Type locality: San Bernardino (Paraguay). Type material: 1 worker (only mesosoma), lectotype designated by KEMPF (1958 a: 32), labelled " San Bernardino, Paraguay, in dry wood,

Cr. pilosus fiebrigi, lectotype, W. W. Kempf det."; 2 workers and 1 soldier (syntypes) labelled „San Bernardino, Paraguay, in Spalten trockenen Holzes (Fiebrig), *C. pilosus* Em. r. *fiebrigi* Forel, type", in MHNG, examined.

Cryptocerus guttifer SANTSCHI, 1919: 45. Soldier and gyne. Original description. Type ocality: Alta Gracia (Córdoba, Argentina). Type material: 1 gyne (syntype) labelled "Córdoba, Ar. Alta Gracia, Bruch, *Cr. guttifer* Sant. type", in NHMB, examined. Synonymy with *fiebrigi* by KEMPF, 1958 a: 28.

Cryptocerus guttifer SANTSCHI, SANTSCHI, 1922: 253. Worker, soldier, gyne, male. Type material: 8 workers, 2 soldiers, 2 gynes, 2 males (all syntypes) labelled " Córdoba, Ar. Alta Gracia, Bruch, *Cr. guttifer*, Sant. type, Z 1", in NHMB; 1 worker and 1 soldier (syntypes) in MCZC; 1 worker, 1 soldier, 2 gynes labelled only "syntypes", in ZSMC, all examined.

Paracryptocerus fiebrigi (FOREL), KEMPF, 1958 a: 28, figs. 1, 11, 17, 27. Worker, soldier, gyne. First combination in *Paracryptocerus*.

Zacryptocerus fiebrigi (FOREL), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Zacryptocerus fiebrigi (FOREL), VIERBERGEN & SCHEVEN, 1995: 168, fig. 11. Worker.

D i a g n o s i s . - A member of the *fiebrigi* clade differing from its sister species, *guayaki*, in the worker, soldier and gyne by the denser, erect, truncate body hairs.

W o r k e r (Fig. 313) (description of KEMPF, 1958 a). - "Total length 3.9–4.9 mm. Black; frontal carinae pale testaceous or pale ferruginous; articulations of legs, tarsi, tips of scapes and basal segments of funiculus, more or less fuscous-ferruginous.

Head subopaque, subrectangular, distinctly longer than broad, its upper face rather convex in the middle, the frontal carinae flat to excavated, the entire surface finely reticulate-punctate, sparsely and rather shallowly foveolate without conspicuous rugosities. Sides of head subparallel, often distinctly concave above eyes. Frontal carinae, in part, translucid, in lateral view considerably thickened just in front of the eyes.

Thorax, in profile, - also transversely across the pronotum, - noticeably convex. Promesonotum less expanded laterad, its sides tridentate, the posterior tooth more or less rectangular. Mesonotum laterally tuberculate or subdentate. Sides of basal face of epinotum bidentate, the posterior tooth being largest. Declivous face sharply marginate at the sides. Sculpture of dorsum of thorax as on head, finely reticulate-punctate and sparsely foveolate. Sides of thorax with finely reticulate-punctate with fine, more or less longitudinal rugosities on the laterotergite of the pronotum. Sides of fore coxae not transversely striate.

Peduncular segments with a triangular anterior face, separated from the dorsal face by a more or less marked edge, the vertex of the anterior face forming middorsally a projecting tooth, facing caudad. This tooth is rather feeble on the petiole, but strongly marked on the postpetiole. Lateral spines of the petiole long, rather delicate, gently and evenly recurved, and acute at apex. Spines of postpetiole similar, but much more strongly recurved. Body of petiole comparatively narrower than in *pilosus*.

Gaster oval, similar to that of *pilosus*, slightly more shining, the first tergite being very finely and rather superficially reticulate-punctate. General pattern of pilosity as in *pilosus*, but the appressed scalelike hair is shorter and finer, and the standing hair is abundant, more scattered, much shorter (shorter than the diameter of tibiae), straight, not visibly flexuous."

Measurements (in mm) and indices: TL 3.64–4.84; HL 0.86–1.06; HW 0.88–1.08; EL 0.25–0.29; PW 0.81–1.00; PeW 0.44–0.56; PpW 0.48–0.59; HBaL 0.40–0.41; HBaW 0.09–0.11; CI 101.9–102.3; PI 108.0–108.6; PPeI 178.6–184.1; PPpI 168.7–169.5; HBaI 18.9–22.5.

S o l d i e r (Fig. 314) (description of KEMPF, 1958 a). - "Total length 5.8–6.5 mm; maximum length of head 1.68–1.78 mm; of thorax 1.57–1.72 mm. Black; the following yellowish-ferruginous: anterolateral portion of head disc, a triangular area on each shoulder, and usually four larger spots on the first gastral tergite, one close to each corner, the pair of the same side often being confluent; ferruginous: tip of scape, first funicular segment, knees, extensor face of tibiae, the four apical tarsites of each leg.

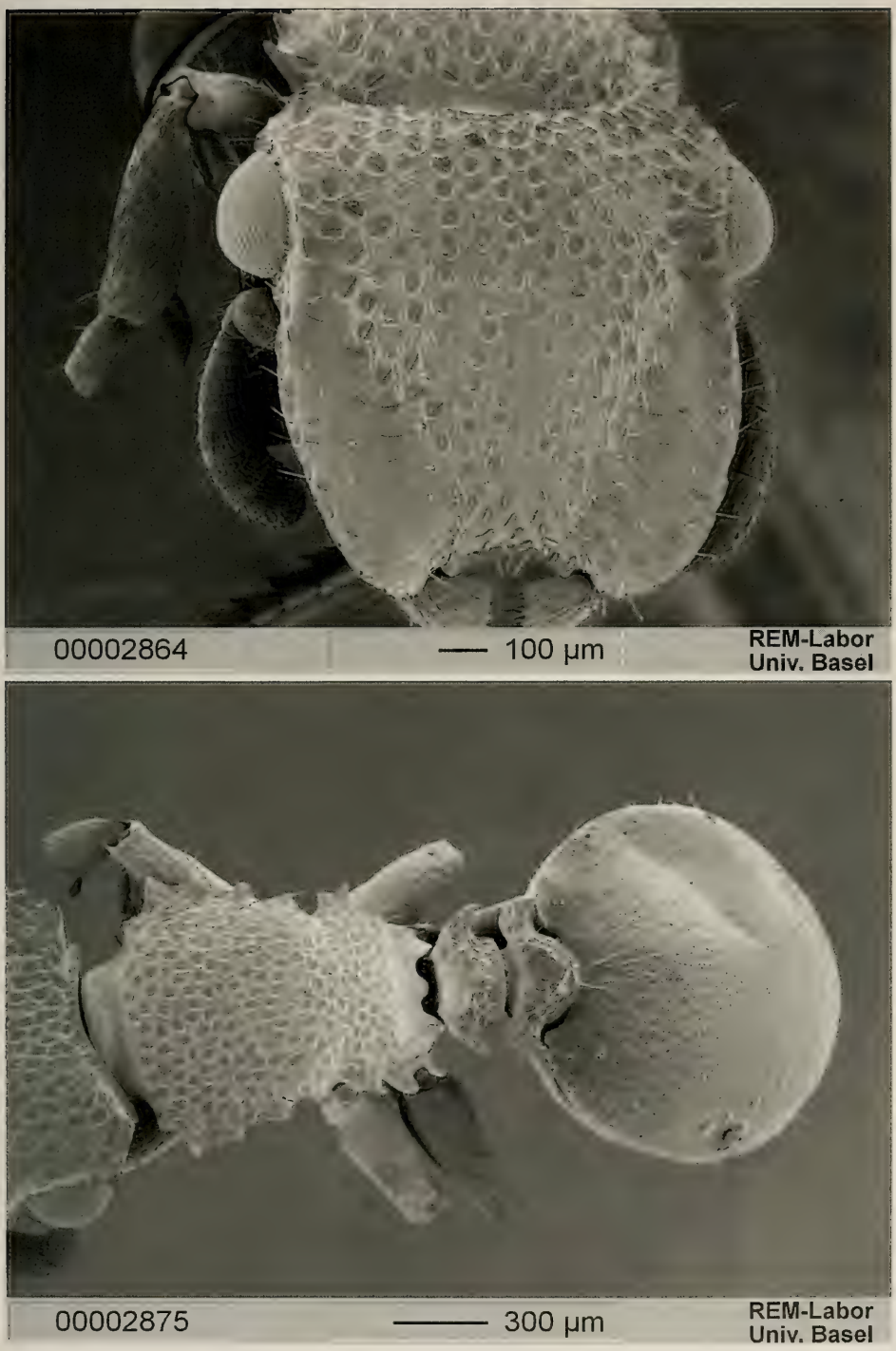


Fig. 313. *Cephalotes fiebrigi* (FOREL). Worker from Itaberaba (Bahia), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

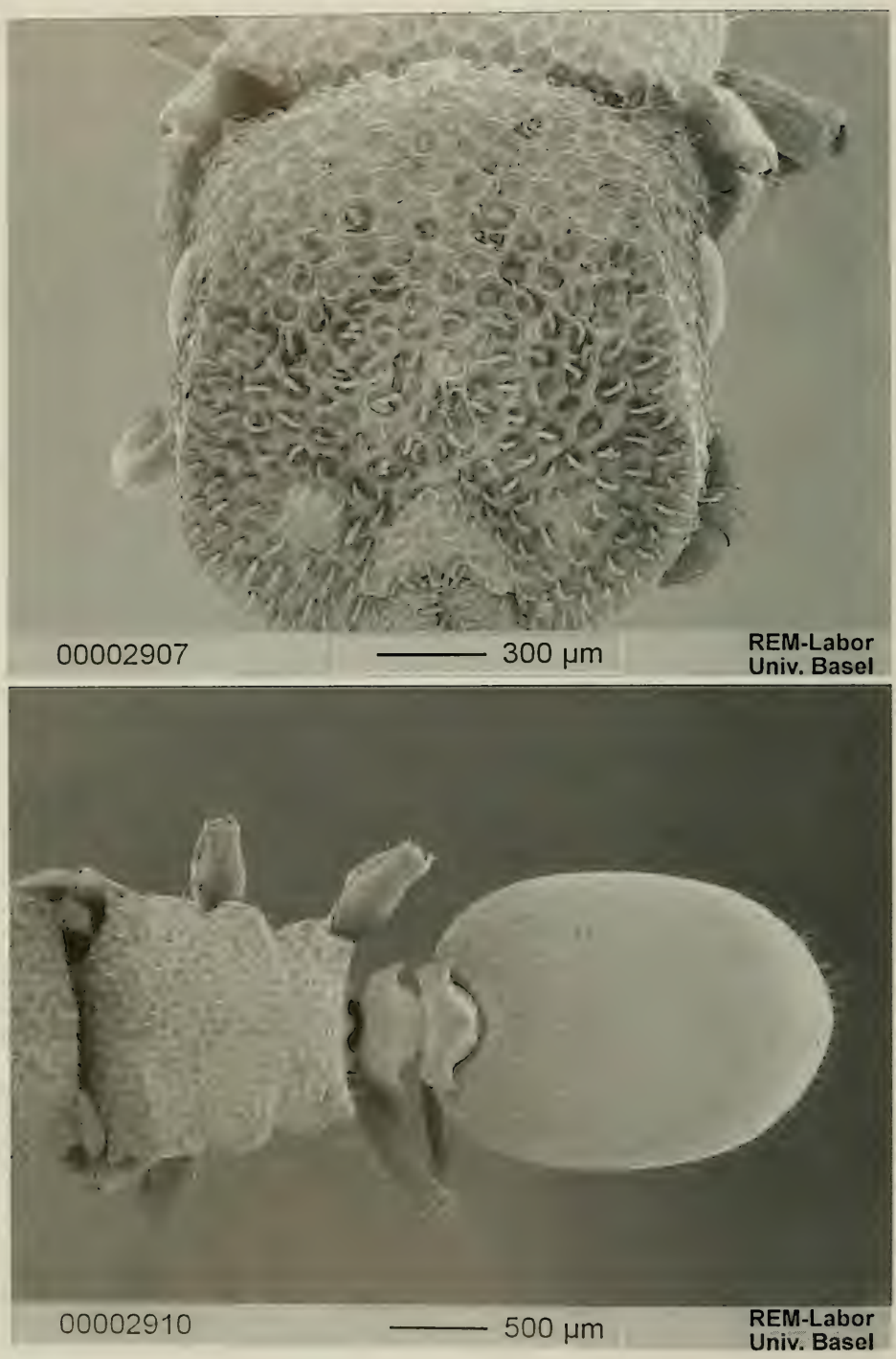


Fig. 314. *Cephalotes fiebrigi* (FOREL). Soldier from Córdoba (Alta Gracia), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

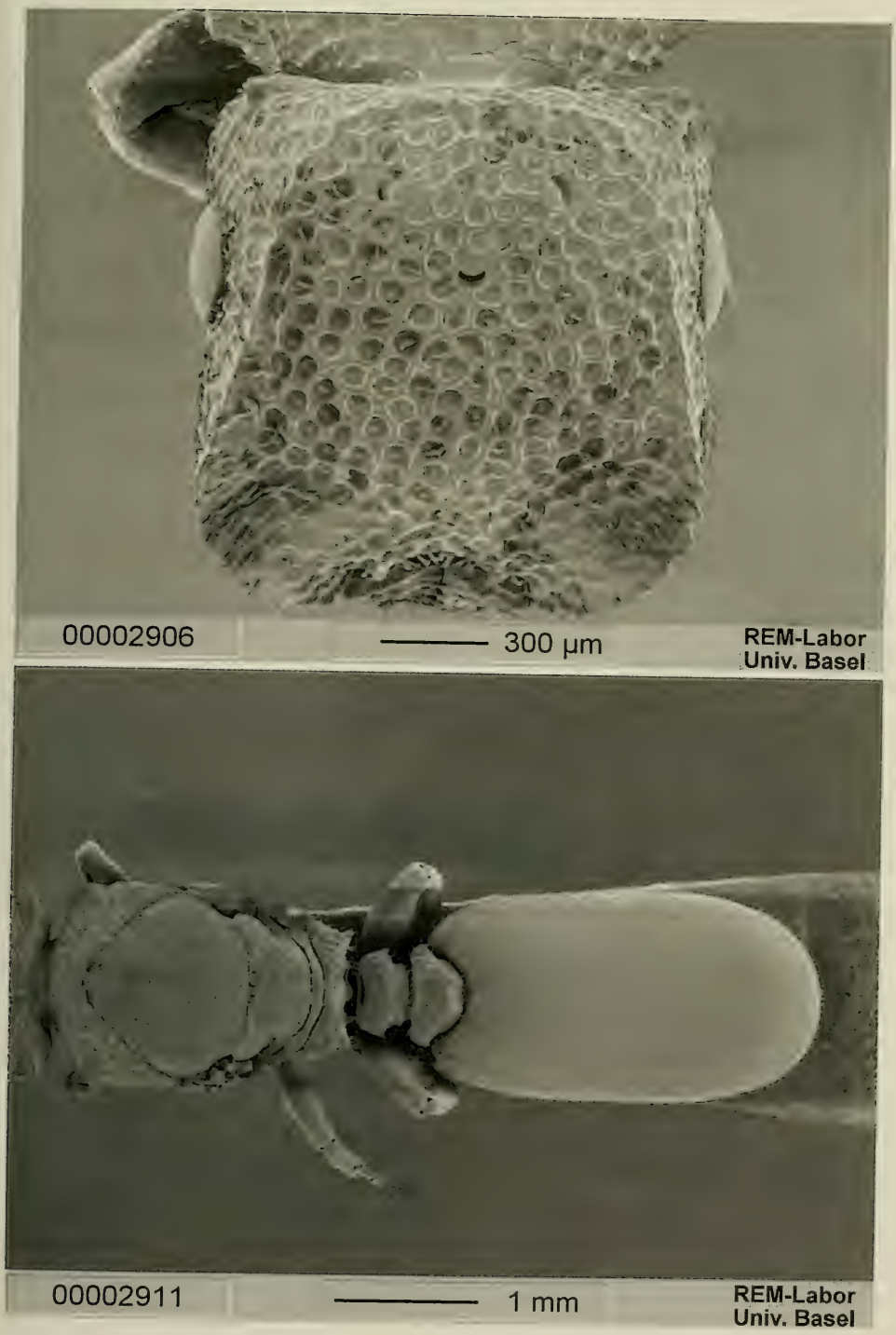


Fig. 315. *Cephalotes fiebrigi* (FOREL). Gyne from Córdoba (Alta Gracia), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

Head disc more elongate, its rim less distinctly crenulate, its sides distinctly converging caudad, with a feeble constriction at the level of the eyes. Anterolateral portion of head disc more or less excavated, the clypeal area marked off by a raised ridge. Sculpture of disc coarsely reticulate-rugose, as in *pilosus*, but the meshes are larger, and the foveolae more deeply impressed. About twelve foveolae may be counted in a transverse row, across the head, at the level of the eyes (fifteen or more in *pilosus* and *liogaster*).

Thorax dorsally mostly foveolate, scarcely reticulate-rugose. Transverse pronotal carina feeble, usually broadly interrupted in the middle, nor forming a raised crest. Laterotergite of pronotum finely and more or less longitudinally rugose. Sides of thorax never with strong rugosities. Sides of fore coxae only reticulate-punctate.

Peduncular segments in general as in worker, broader than in *pilosus*, with strong lateral spines. Only the postpetiole possesses a sharply edged triangular anterior face, the vertex of which terminates middorsally in a tooth. Sides of gaster gently convex. The first tergite finely but superficially reticulate-punctate, with a few longitudinal rugosities on the antero-median portion.

Pilosity, in general, as in worker. In addition the following highly distinctive feature: from each foveola of the head disc and the sides of head emerges a thick, curved scalelike hair, the free end of which projects well beyond the rim of the foveola. A somewhat similar condition holds occasionally for the foveolae of the thorax."

Measurements (in mm) and indices: TL 5.92–6.60; HL 1.48–1.52; HW 1.44–1.48; EL 0.33–0.35; PW 1.40; PeW 0.68–0.69; PpW 0.69–0.77; HBaL 0.39–0.41; HBaW 0.11; CI 94.7–100.0; PI 102.8–105.7; PPeI 202.9–205.9; PPpI 181.8–202.9; HBaI 26.8–28.2.

G y n e (Fig. 315) (description of KEMPF, 1958 a). - "Total length 7.5–7.9 mm; maximum length of head 1.67–1.71 mm; of thorax 2.14–225 mm. Color, sculpture and general features as in soldier. The head disc is still more elongate, indistinctly marginate postero-laterally behind the eyes. It differs from *pilosus* and *liogaster* by the shape of the peduncular segments, the nearly parallel-sided gaster, the short wings. The fore wing, measuring 5.1–5.2 mm, projects very little beyond the tip of the gaster, when folded over the back. The wings are infuscated, the venation of the fore wing is quite similar to that of *liogaster*."

Measurements (in mm) and indices: TL 7.88–7.92; HL 1.48–1.52; HW 1.40–1.48; EL 0.36; PW 1.36–1.40; PeW 0.59–0.60; PpW 0.68–0.73; HBaL 0.49–0.51; HBaW 0.12–0.13; CI 94.6–97.4; PI 102.0–102.1; PPeI 226.7–237.3; PPpI 191.8–200.0; HBaI 24.5–25.5.

M a l e (previously undescribed). - Very similar to the male of *pilosus* and *lanuginosus* but differing from both in the following details: Head more convex dorsally. Eyes as broad as in *pilosus* and smaller than in *lanuginosus*. Anterior face of the petiole concave as in *lanuginosus*. Hind basitarsi longer and narrower than in *pilosus* and *lanuginosus*.

Sculpture. First gastral tergite as shining as in *lanuginosus*. Rugosities on the propodeal dorsum irregular on the sides and slightly transversal on the middle, those on the pedicel regular and very superficial.

Pilosity. Hairs flexuous as in *lanuginosus*.

Colour. Black, gaster slightly lighter. Coxae and two proximal thirds of the femora light brown. Distal third of femora, tibiae and tarsi dark yellow.

Genitalia and subgenital plate as in Fig. 316.

Wings as in Fig. 317.

Measurements (in mm) and indices: TL 5.60–5.76; HL 0.84–0.94; HW 0.98–1.04; EL 0.43–0.46; PW 0.96–1.02; PeW 0.50–0.56; PpW 0.55–0.63; HBaL 0.48–0.51; HBaW 0.09; CI 110.6–116.7; PI 101.9–104.0; PPeI 178.6–192.0; PPpI 161.9–174.5; HBaI 17.6–18.7.

M a t e r i a l e x a m i n e d. - **Brazil**: P i a u í: 10 km N of Corrente, Fazenda Maracujá, 23–27.XI.1991, 1 gyne, C. R. F. BRANDÃO [MZSP]. B a h i a: Itaberaba, Fazenda Riacho do Uruçu, 1–5.XII.1990, 11 workers, 1 soldier, C. R. F. BRANDÃO et al. [MZSP]. M a t o G r o s s o d o S u l: Imbirussú-Corumbá, 01.XII.1960, 4 workers, K. LENKO [MZSP].

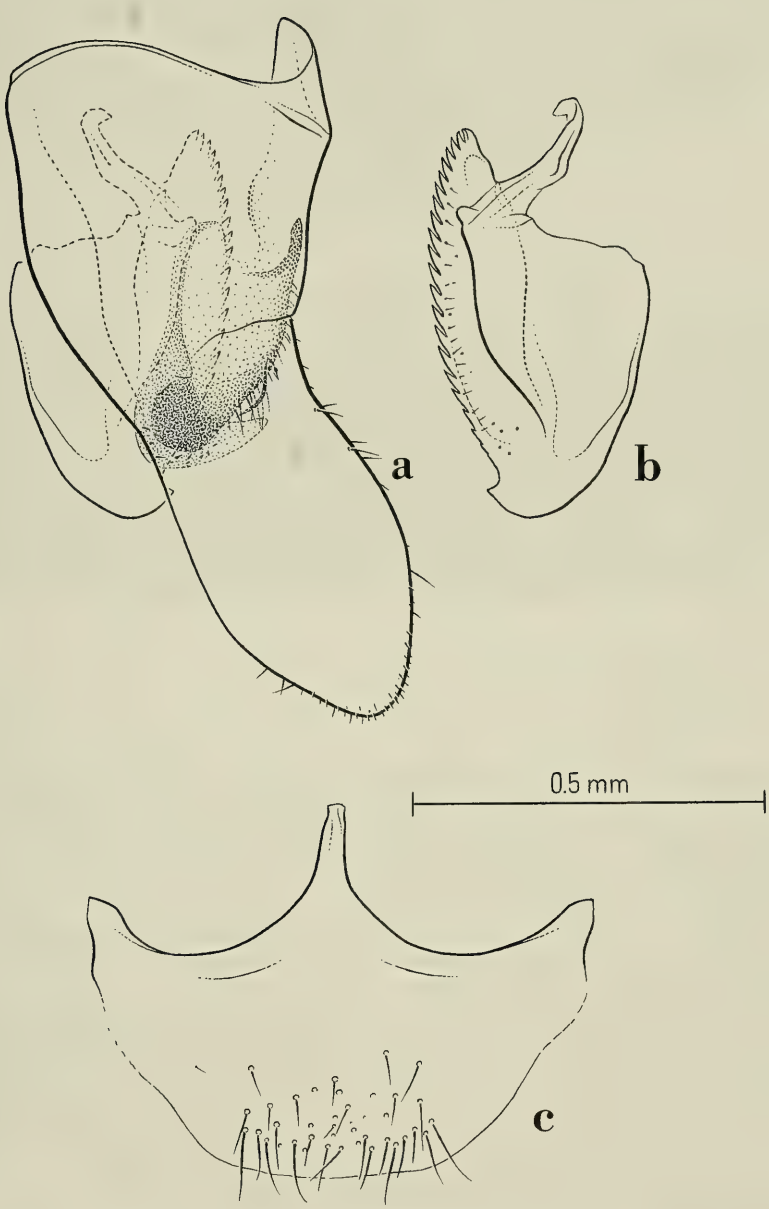


Fig. 316. *Cephalotes fiebrigi* (FOREL). Male from Córdoba (Alta Gracia), Argentina. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

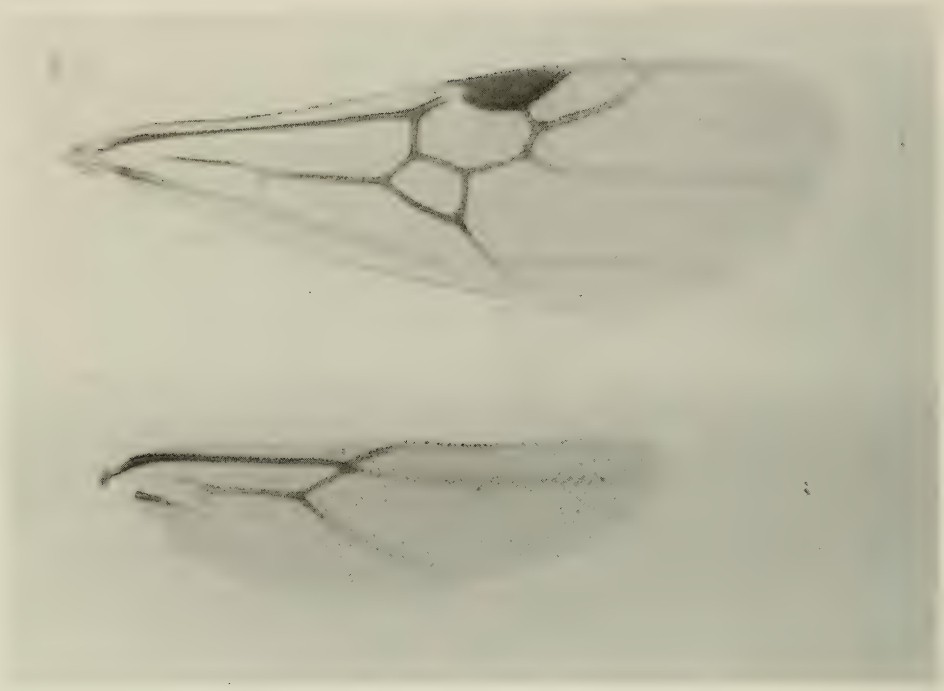


Fig. 317. *Cephalotes fiebrigi* (FOREL). Male from Córdoba (Alta Gracia), Argentina, fore and hind wings.

Argentina: Córdoba: Alta Gracia, 9 workers, 3 soldiers, 3 gynes, 2 males, (all syntypes of *guttifer*), BRUCH [NHMB, MCZC]; Alta Gracia, La Granja, Sierras de Córdoba, 03.II.1925, 2 workers, 2 soldiers, 2 gynes, 2 males (partly labelled as syntypes), C. BRUCH [MZSP]; same locality, 1 soldier, DAGUERRE [USNM]. Tucumán: no further locality, 1 worker (syntype of *Ellenriederi* var. *tucumana*), SHIPTON [MHNG]. Salta: Las Termas, 13.XII.1947, 1 gyne [MZSP].

Paraguay: La Cordillera: San Bernardino, 3 workers, 1 soldier (lectotype and paratypes of *fiebrigi*), in dry wood, FIEBRIG [MHNG]. Alto Paraná: Pastoreo, XI-XII.1974, 1 gyne, P. DUELLI [MZSP].

Discussion. - One of the two syntypes of the unavailable name *tucumana* preserved in MHNG and synonymised with *bivestitus* by KEMPF (1958 a) must be referred to *fiebrigi*. The second syntype examined by us actually corresponds to *bivestitus*. On the other hand, *guttatus* var. *trivialis* SANTSCHI tentatively synonymised with *fiebrigi* by KEMPF (l. c.) must be referred to *bivestitus*.

The Brazilian specimens we examined are more opaque than the others available for the present study.

C. fiebrigi, *guayaki* and *quadratus* share by synapomorphy the erect, truncate hairs, on the whole body of *fiebrigi* and *guayaki* and restricted to the gaster and legs in *quadratus*.

As we already stated for other species of the *fiebrigi* clade, the pilosity appears to be one of the main characters useful to separate the species of this clade.

Distribution: Brazil, Argentina, Paraguay.

5.6.23. The *prodigiosus* clade

A small clade containing only two Argentinean species characterised by having soldiers with the cephalic disc concave and with irregular foveae bearing clavate hairs not surpassing the border of the foveae. The gynes of both species are also unique in the shape of the disc: concave in the two anterior thirds and flat posteriorly. Both species appear to be rather rare: fewer than 20 specimens are known.

Species included in the clade: *bivestitus*, *prodigiosus*.

Cephalotes prodigiosus (SANTSCHI) new combination

Cryptocerus prodigiosus SANTSCHI, 1921 b: 124. Soldier, gyne. Original description. Type locality: Río Salado and Río Dulce, both near Icaño (Santiago del Estero, Argentina). Type material: the lectotype soldier selected by KEMPF, 1964 b: 252 cannot be found in the NHMB, one syntype soldier from Río Dulce in NHMB (examined), one syntype soldier labelled: "Chaco de Santiago del Estero, Bords du Río Salado, Env. D' Icaño, E. R. Wagner, 1914. Type unique. *Cryptocerus prodigiosus* Sant., soldier, type, SANTSCHI det. 1921" (examined); one syntype gyne, same label as the second paratype soldier but differing in the date of collection: 1910. *Cryptocerus prodigiosus* SANT., gyne, type, SANTSCHI det. 1921 (examined), both paratypes in MNHN.

Paracryptocerus prodigiosus (SANTSCHI), KEMPF, 1958 a: 49. First combination in *Paracryptocerus*.

Paracryptocerus prodigiosus (SANTSCHI), KEMPF, 1964 b: 252, fig. 13. Soldier.

Zacryptocerus prodigiosus (SANTSCHI), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *prodigiosus* clade. The soldier is recognisable from that of *bivestitus* (the sole other species in this clade) by the large body size, by the head dorsum almost completely concave and by the apomorphic loss of the longitudinal carina in front of the eyes. The gyne differs from that of *bivestitus* by the broad, deep, irregular foveae on the cephalic dorsum.

S o l d i e r (description of KEMPF, 1964 b). - "Total length 10.7 mm; maximum length of head 3.05 mm; maximum width of head 2.95 mm; Weber's length of thorax 3.00 mm. Black; upper half of sides of head, cephalic disc, shoulders, tip of epinotal teeth, extensor face of tibiae, four apical tarsites more or less brownish red.

Head opaque, finely reticulate-punctate, about as broad as long, surmounted by a broadly ovoid, deeply excavate, completely marginate saucerlike disc, having the posterior border evenly rounded, the anterior border excised above the reticulate-rugose mandibles; floor of disc with a prominent convexity just in front of the middle, not visible in side-view, being concealed by the strongly upturned lateral rim of the disc. The latter finely crenulate, not conspicuously upturned posteriorly nor overhanging the flat occiput. Clypeal sutures not evident. Eyes rather flat, scarcely visible from above. Antennal scrobe reaching the eye. Inferior border of cheeks marginate, extending back to the likewise marginate and bluntly dentate occipital lobes. Floors of disc and sides of head coarsely and densely reticulate rugose with deeply impressed and rather irregular pits within the meshes. Gular face less coarsely sculptured, areolate-rugose, the intervals between the shallower foveolae being blunt, not forming sharp and raised ridges.

Thorax opaque, finely reticulate-punctate. Pronotum greatly expanded laterad, the anterior angle of the expansion dentate, followed by a short blunt lobe in front of the prominent, mesially interrupted transverse pronotal crest. Pronotum not excavate laterally in front of crest. Promesonotal suture vestigial, not impressed. Mesonotum rather flat in both directions, each side with a projecting and broadly rounded lobe. Mesoepinotal suture impressed. Basal face of epinotum transversely convex with a short blunt, lateral lobe and a

subacute, upturned posterior tooth. Declivous face shallowly excavate, laterally submarginate, lacking macro-sculpture. Femora fusiform. Dorsum of thorax reticulate-rugose and foveolate, but the sculpture is not as coarse as on cephalic disc. Sides of thorax similarly sculptured, but the foveolae are more elongate and shallower, the horizontal rugae becoming gradually more prominent toward the bottom. Extensor face of femora lightly reticulate-rugose.

Petiole and postpetiole opaque, irregularly reticulate-rugose and foveolate, each segment bearing laterally a beaklike appendage, pointing backwards and, on the postpetiole, also slightly upwards. Petiole with a subvertical anterior face distinct from the horizontal upper face. Postpetiole, in profile, strongly convex with a dorsal peak formed by a pair of tumuli. Gaster subopaque, elongate, about 1.5 times as long as broad, anterolaterally strongly lobate, the lobes immarginate. Tergum I finely reticulate-punctate and covered with sparse and shallow foveolae, becoming superficial to obsolete towards the rear. Sternum I superficially areolate-rugose.

Gular face of head, thorax, pedicel and legs with golden decumbent or appressed, elongate, canaliculate, scalelike hairs. The same hairs on anterior end of gaster, becoming gradually finer and shorter toward the rear. Cephalic disc, sides of head, and anterior portion of pronotum in front of transverse crest with thick, recurved or suberect short hairs, which lack the metallic sheen. Hairs in pits on cephalic disc do not project beyond the rim of the foveolae from which they arise. Rim of cephalic disc laterally with a few widely spaced very short and blunt projecting hairs."

Measurements (in mm) and indices: TL 10.12–10.56; HL 2.60–2.64; HW 2.72–2.76; EL 0.44–0.48; PW 2.56–2.64; PeW 0.91–1.00; PpW 1.04–1.10; HBaL 0.68–0.70; HBaW 0.20–0.22; CI 104.5–104.6; PI 104.5–106.2; PPeI 264.0–281.3; PPpI 240.0–246.1; HBaI 29.4–31.4.

G y n e . - Head subquadrate, with disc. Anterior two-thirds of the head concave; posterior third almost flat. Frontal carinae with crenulate margin, broadly expanded anteriorly, with raised border, converging posteriorly and connected by a convex ridge on the vertex. Vertexal angles round and with clearly differentiate margin. Eyes convex and partially hidden by the disc in dorsal view. Anterior clypeal border concave. Mandibles laterally carinate and partially hidden by the frontal carinae.

Mesosoma dorsally flat in profile. Humeral angles with an obtuse tooth anteriorly, straight posteriorly. Pronotal crest superficially marked and interrupted in the middle. Promesonotal suture impressed. Propodeum with differentiate basal and declivous faces; basal face weakly convex laterally and ending in a stout, obtuse tooth slightly curved laterally; sides of the declivous face converging posteriorly.

Petiole with distinct anterior and posterior faces; anterior face almost vertical and bearing a pair of lateral denticles dorsally; posterior face sloping posteriorly. Petiolar sides with a small denticle medially. Postpetiole broadly convex and with a superficial concavity in the middle; postpetiolar spines broad, with pointed tip, arising from the anterior border of the postpetiole and gently curved backwards.

Legs. Mid and hind femora not angulate nor denticulate. Mid and hind tarsi not flattened laterally and without broad base.

Gaster with broad, anteriorly protruding lobes.

Sculpture. Head dorsum superficially punctate and covered with dense, broad, deep, irregular foveae diminishing in size anteriorly. Mesonotum and pedicel minutely microsculptured and with dense foveae with thick margins, the foveae smaller on the upper mesopleurae and the pedicel. Declivous face of the propodeum, gaster, legs and upper metapleurae reticulate; the same sculpture but less impressed on the first gastral sternite. Outer face of the tibiae with oval and superficial foveae.

Pilosity. Body with five types of hairs: (1) suberect, clubbed hairs arising from each fovea of the head dorsum and pronotum; (2) hairs similar to the type (1) but subdecumbent on the ventral part of the head; (3) mesonotum, scutellum, propodeum, pedicel, legs and gaster with appressed, slightly clubbed hairs, shorter on the gaster and legs, denser on the outer face of the legs; (4) variably clubbed, erect, sparse hairs, long on the ventral part of the first gastral

sternite, longer on the border of the tergites and sternites, short and rare on first gastral tergite; (5) truncate, long, rare hairs on the posterior border of the sternites.

Colour. Head dorsally and laterally light orange, with lighter frontal carinae. Head ventrally, meso- and metapleurae, ventral part of the propleurae and scutellum brown. Lateral part of the pronotal dorsum, dorsal half of the propleurae and outer face of the femora light orange. Center of the pronotum and mesonotum light brown with yellow-orange maculae. Propodeum, pedicel and legs reddish brown. Gaster ferrugineous and with two pairs of yellow spots: the first pair oval and on the anterior lobes and the second one, round, before the posterior border of the first gastral tergite.

Measurements (in mm) and indices: TL 11.66; HL 2.32; HW 2.40; EL 0.41; PW 2.28; PeW 1.02; PpW 1.20; HBaL 0.72; HBaW 0.22; CI 103.4; PI 105.3; PPeI 223.5; PPpI 190.0; HBaI 31.4.

Material examined. – **Argentina**: Santiago del Estero: Icaño, border of Río Salado, 1 soldier and 1 gyne (syntypes), E. R. WAGNER [MNHN]; same, locality, Río Dulce, 1 soldier (syntype) [NHMB].

Discussion. - The soldier of *prodigiosus* shares with that of *bivestitus*, the only other species in the same clade, the colour, the large, deep foveae on the head dorsum and the propodeum with a pair of stout spines curved upwards. The gynes of both species share the head disc concave in the anterior two thirds, flat in the posterior third and the body colour, orange with darker gaster. This imperfectly known species is the largest among those with disc bearing soldiers.

Distribution: Argentina.

Cephalotes bivestitus (SANTSCHI) new combination
Figs. 318, 319, 320, 321

Cryptocerus bivestitus SANTSCHI, 1922: 254. Worker and gyne. Original description. Type locality: Hualfín (Catamarca, Argentina). Type material 5 workers, 3 soldiers, 4 gynes (all paratypes) labelled "Catamarca, Hualfín (Weiser), *Cryptocerus bivestitus*, Sant. type", in NHMB; 1 worker with additional label "Co- (topo) type, bivestitus paratypus, Kempf det.", in MZSP, examined.

Cryptocerus peltatus Ellenriederi FOREL, FOREL, 1914: 281, partim. Misidentification.

Cryptocerus peltatus Ellenriederi FOREL, BRUCH, 1916: 321, partim, ?fig. 13 (could be also *jheringi*), pl. 9, fig. 14. Worker. Synonymy with *bivestitus* proposed by KEMPF (1958 a: 50) and confirmed by our examination of part of the relevant material.

Cryptocerus guttatus (sic) var. *trivialis* SANTSCHI, 1929: 301. Worker. Original description. Type locality: Chafinian (Catamarca, Argentina). Type material: Holotype (unique) in NHMB, examined. Synonym of *fiebrigi* according to KEMPF (1958 a: 28). New synonym.

Paracryptocerus bivestitus (SANTSCHI), KEMPF, 1958 a: 30, figs. 7, 13, 15. Worker, soldier and gyne. First combination in *Paracryptocerus*.

Zacryptocerus bivestitus (SANTSCHI), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *prodigiosus* clade differing from *prodigiosus*, in the soldier and gyne, by the smaller size, in the soldier only, by the floor of the disc not completely concave, and in the gyne only, by the cephalic foveae, more regular.

Worker (Fig. 318) (description of KEMPF, 1958 a). - "Total length 4.5–4.9 mm; maximum length of head 1.25–1.39 mm; of thorax 1.25–1.39 mm. Black; frontal carinae testaceous. Tips of mandibles, scapes, extensor face of tibiae, apical tarsites ferruginous or fuscous-ferruginous.

Head subopaque, rectangular, visibly longer than broad. Cephalic index (maximum width as measured in front of the eyes over maximum length as measured from the anteriormost point of frontal carinae to posteriormost point of occipital lobes) 0.82–0.86. Mandibles finely rugulose. Frontal carinae semitrasparent, without a distinctly crenulate border, straight, not conspicuously emarginate in front of, nor upturned above the eyes, very gently diverging caudad. Occipital corners obliquely truncate; occipital border shallowly emarginate. Eyes small, their greatest diameter less than one fourth of maximum head length. Upper face of head gently and evenly convex, finely reticulate-punctate, more sparsely covered with shallow, squamiferous foveolae, which occur somewhat more densely and larger towards occiput. Between the foveolae most specimens show more or less longitudinal yet rather fine rugosities. Vertex without a pair of small denticules. Lower face of head reticulate-rugose, the rugae forming elongate meshes.

Thorax subopaque. Anterior border moderately arcuate. Scapular angle subdentate, not well visible from above, lying beneath the anterior corner of the pronotal crest. This crest bears anteriorly an acute, strong tooth, followed by two or three blunt, crenate or denticulate lobes. Occasionally, the first lobe may have the form of a tooth, yet a distinctly tridentate condition of the lateral crest is rare. Promesonotal suture effaced. Sides of mesonotum angulate or even feebly dentate. Promesonotum moderately convex both in profile and transversely. Mesoepinotal suture absent. Anterior corner of basal face of epinotum forming a rectangular tooth, followed by another larger triangular tooth on the sides. Sides of declivity sharply marginate, the edge bearing one or several minute teeth. Basal face and declivity, as seen from the side, form an even but gentle curvature. Dorsum of thorax sculptured as head, finely reticulate-punctate, rather densely covered with squamiferous foveolae. The slightly raised intervals between the foveolae form a network of anastomosing rugosities, which are more conspicuous on thorax than on dorsum of head. Lowermost portion of declivous face finely reticulate-punctate. Laterotergite of pronotum with a few horizontal striae. Thoracic pleura finely reticulate-punctate and more coarsely rugose.

Peduncular segments subequal in width. Petiole dorsally without a transverse carina, but bearing on each side a strong pointed tooth, pointing obliquely caudad. Postpetiole with a dorsally submarginate, inclined anterior face, and with lateral spines, the tip of which is strongly recurved, acute, pointing directly caudad.

Gaster subopaque, oval. Strongly emarginate antero-mesally, the anterolateral lobes almost semicircular, solid, without a distinctly marginate border. First tergite extremely finely reticulate-punctate. A few longitudinal but short rugosities extending from the postpetiolar insertion caudad. Squamiferous foveolae very shallow and sparse.

Dorsum of head, thorax, and peduncular segments bearing in the foveolae appressed, silvery, canaliculate, scalelike hair. Similar hair bit simple, on the first gastral tergite. Standing hair, as usual, confined to the posterior and ventral face of gaster."

Measurements (in mm) and indices: TL 4.38–5.24; HL 1.02–1.26; HW 1.10–1.36; EL 0.30–0.33; PW 0.96–1.12; PeW 0.49–0.59; PpW 0.50–0.60; HBaL 0.39–0.45; HBaW 0.09–0.10; CI 103.6–107.9; PI 114.6–121.4; PPeI 178.2–195.9; PPpI 175.0–192.0; HBaI 22.5–25.6.

S o l d i e r (Fig. 319) (description of KEMPF, 1958 a). - "Total length 7.3–8.0 mm; maximum length of head 2.10–2.25 mm; of thorax 1.89–2.03 mm. Black; the following ferruginous: head disc, (excepting the black clypeal and frontal region), sides of head, legs (usually more or less infuscated); yellowish-brown: triangular area on each shoulder, lateral borders of mesonotum, extensor face of tibiae. The four spots of the first gastral tergite pale-testaceous.

Head somewhat shining; longer than broad, surmounted by an elongate, completely marginate disc, which is much broader in front than behind, its sides converging caudad, with a feeble constriction near the level of the eyes, its posterior border evenly rounded. The anterior four fifths of the cephalic disc form a circular, pronouncedly excavate area, with strongly raised, scarcely crenulate lateral borders. The center of the excavation, coinciding with the vestigially limited clypeal and frontal area, slightly raised and convex. The posterior fifth of the head disc, which is sickle-shaped, is flat, with narrowly crested lateral and posterior border. Mandibles strongly reticulate-rugose. Eyes feebly convex, scarcely visible

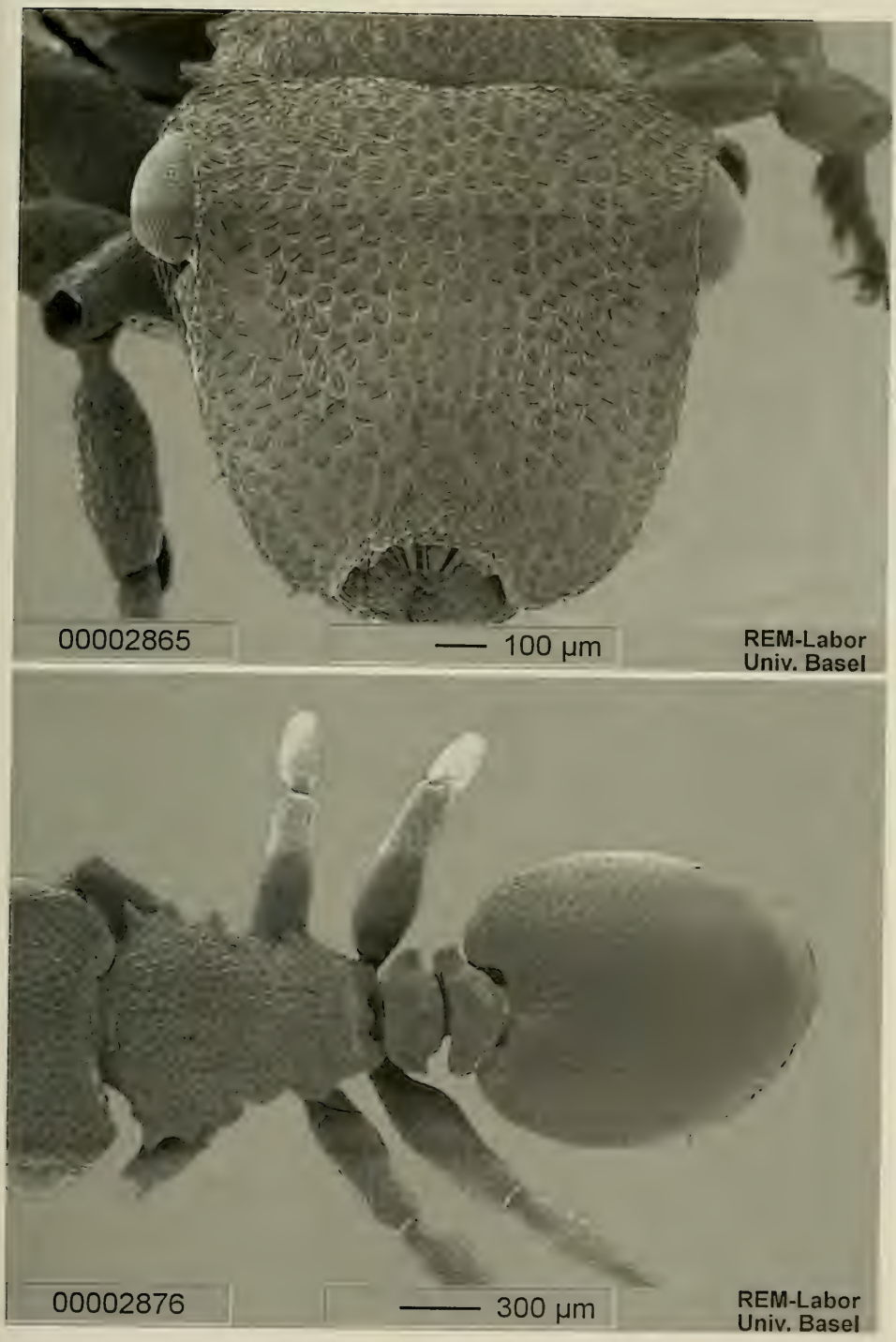


Fig. 318. *Cephalotes bivestitus* (SANTSCHI). Worker from Represa del Carmen (San Luís), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

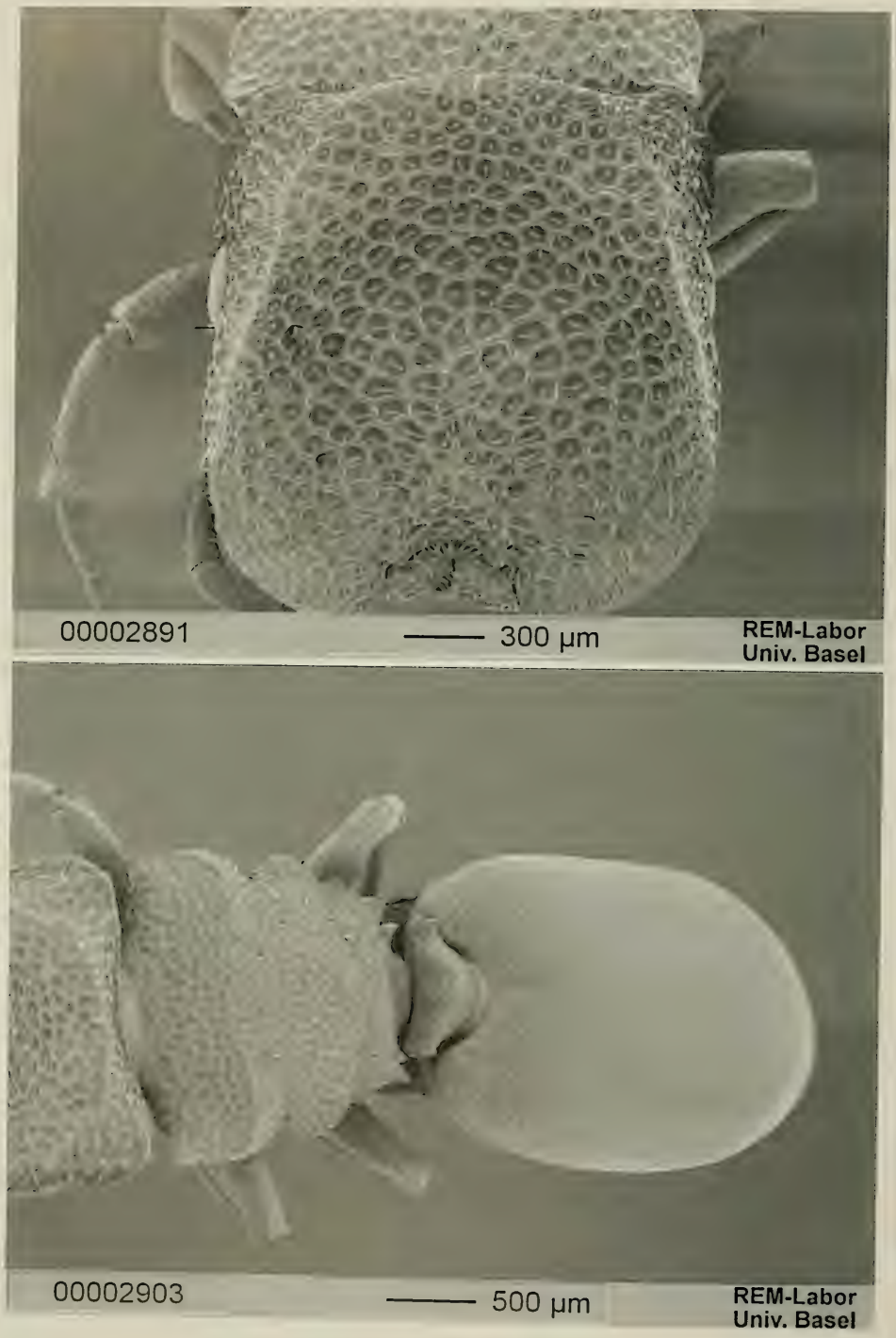


Fig. 319. *Cephalotes bivestitus* (SANTSCHI). Soldier from Hualfin (Catamarca), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

from above, being partly covered by the head disc. In side view, the dorsal face of the head disc invisible, being concealed by the sides of the disc. Lower border of cheeks carinate. Occipital lobes bluntly angulate, with rounded, carinate borders. Floor of head disc and sides of head coarsely reticulate-rugose, with deeply impressed, circular, large foveae, the bottom of which is shining. About 18 foveae may be counted along a line drawn transversely across the head disc, at the level of the eyes. Lower face of head more shining, with coarser rugosities and more spaced foveolae.

Thorax slightly shining, compact. Anterior corner of pronotum dentate, its sides subparallel until reaching the weakly crested, mesally interrupted transverse carina. From this point the sides gently converge caudad toward the mesonotum. Promesonotal suture distinct. Mesonotum having on each side a projecting, bluntly rounded, posteriorly marginate, lobe. Mesoepinotal suture scarcely impressed mesially. Basal face of epinotum about three times as broad, as long along the midbody line, having a short, bluntly rounded tooth on each side, and another more pronounced tooth on each posterior corner. Declivous face less than twice as long as basal face, feebly marginate at the sides. Sculpture of thoracic dorsum as on head disc, yet the rugosities are broader, the foveolae smaller, less deeply impressed and often somewhat elongate, especially on mesoepisternum. Laterotergites of pronotum with oblique striation. Remaining parts of the sides of the thorax reticulate-rugose, with horizontally elongate, shallow foveolae. Declivous face reticulate-punctate.

Peduncular segments slightly shining, with the dorso-lateral sculpture as on dorsum of thorax. Petiole as broad as postpetiole, its anterior face, which is nearly vertically truncate, finely reticulate-punctate, its sides with a strong, short spine, pointing obliquely caudad. Postpetiole with strong lateral processes, which are strongly recurved and resemble the beak of an eagle. Anterior face of postpetiole somewhat inclined, meeting the dorsal face at angle, which separates both faces by a weakly marginate transverse carina.

Gaster subopaque, elliptical, elongate, with subparallel sides, strongly emarginate antero-mesally, the projecting anterolateral lobes with immarginate border. First gastral tergite reticulate-punctate, with sparse, shallowly impressed squamiferous punctures. A few more or less longitudinal and widely spaced rugosities on the anterior portion of the first tergite.

Foveolae of the head disc and sides of head, with a central, scalelike, curved, thick hair, the tip of which projects beyond the rim of the pit, as in *fiebrigi*. Rim of head disc with projecting clavate setae. Scalelike hair of thorax and gaster appressed, smaller, silvery, smallest on gaster. Standing hair, as usual, only on the tip and venter of gaster."

Measurements (in mm) and indices: TL 7.48–7.72; HL 1.80; HW 1.80–1.82; EL 0.35–0.36; PW 1.72; PeW 0.78–0.81; PpW 0.80–0.81; HBaL 0.48–0.50; HBaW 0.13–0.15; CI 100.0–101.1; PI 104.6–105.8; PPeI 212.3–220.5; PPpI 212.3–215.0; HBaI 27.1–30.0.

G y n e (Fig. 320) (description of KEMPF, 1958 a). - "Total length 8.2–8.8 mm; maximum length of head 1.85–2.03 mm; of thorax 2.36–2.50 mm. Diagnostic features as in soldier. The lightly colored parts (head disc, sides of head, shoulders, extensor face of tibiae) are orange instead of ferruginous, but the center of head disc is much more extensively infuscated. Portions overlying the antennal scrobe transparent in part. Head disc with an anterior circular excavation, which is much shallower than in soldier, with the lateral borders less strongly raised, but more conspicuously crenulated. The posterior fifth of head disc transversely convex, in l ateral view distinctly sloping downward toward occiput, forming a very obtuse, yet visible angle with the anterior portion. Occipital border nearly straight and sharply marginate. Ocelli minute, the antero-median ocellus being located in the excavate portion of head disc, the two postero-lateral ocelli in the posterior portion, facing obliquely caudad and laterad. Thorax less elongate than in *fiebrigi*, the sides of the pronotum slightly diverging caudad. Scutum broader than long. Mesopleural tooth obtuse, yet distinguishable. Peduncular segments similar to those of *fiebrigi*. Gaster more deeply emarginate antero-mesally, the anterolateral lobes rounded. Sides of gaster subparallel. Wings subhyaline, only slightly infuscated, the venation as in *fiebrigi*. Fore wings, when folded over the back, distinctly project beyond the posterior tip of the gaster."

Wings as in Fig. 321.

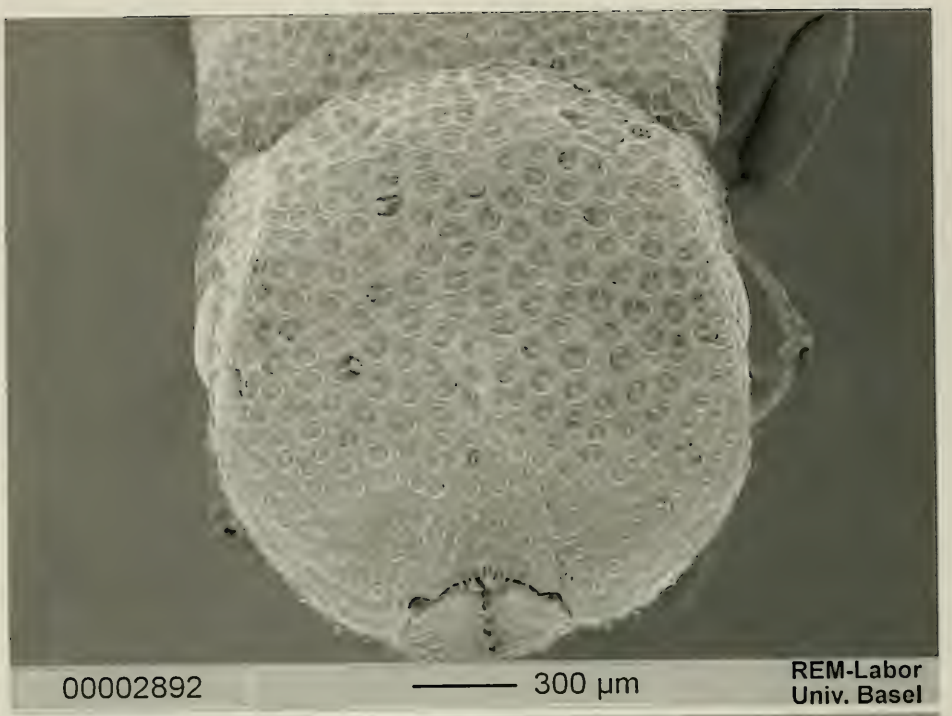


Fig. 320. *Cephalotes brevistitus* (SANTSCHI). Gyne from Hualfin (Catamarca), Argentina: head (top) and meso- and metasoma (bottom) in dorsal view.

Fig. 321. *Cephalotes bivestitus* (SANTSCHI). Gyne from Hualfin (Catamarca), Argentina, fore and hind wings.

Measurements (in mm) and indices: TL 8.36–8.80; HL 1.64–1.68; HW 1.56–1.64; EL 0.36; PW 1.52–1.56; PeW 0.64–0.66; PpW 0.72–0.79; HBaL 0.55–0.56; HBaW 0.12; CI 95.1–97.6; PI 102.6–105.1; PPeI 236.4–237.5; PPpI 197.5–211.1; HBaI 21.4–21.8.

Material examined. – **Argentina**: Formosa: Las Lomitas, 1 worker, N. KUSNEZOV [MZSP]. Catamarca: Hualfin, 6 workers, 3 soldiers, 4 gynes, (all syntypes), WEISER [NHMB, MZSP]; Chafinian, Valde, 09.I.1922, 1 worker (type of *guttifer trivialis*), WEISER [NHMB]; Nacimiento, 20.XII.1922, 1 worker, WEISER [MZSP]; Amando, 17.I.1923, 2 workers [MZSP]; La Cienaga, 1 soldier, WEISER & WOLTERS [MZSP]. Tucumán: Tucumán, 1 worker (syntype of *peltatus ellenriederi* var. *tucumana*), SHIPTON [MHNG]. La Rioja: no further locality, 1 gyne, C. BRUCH [MZSP]. San Luís: no further locality, 1 worker, C. BRUCH [MZSP]; Represa del Carmen, Alto Pencoso, in a branch of *Prosopis*, 1 worker, C. BRUCH [MHNG].

Discussion. - One of the two syntypes of the unavailable name *tucumana* must be referred to this species (the other syntype has been already discussed under *fiebrigi*). One of the two workers identified as *ellenriederi* by FOREL (1914) equally refers to *bivestitus* (the other one is *supercilii*). The morphological uniformity of all the specimens we refer to *bivestitus* represents an additional reason to maintain its insufficiently known sister species, *prodigiosus*, as a good species.

Distribution: Argentina.

5.6.24. The *angustus* clade

A relatively large clade comprising 10 species characterised by combinations of characters present homoplastically also in other clades and secondarily lost in a few ingroup species. Two of these characters appear as synapomorphic in our phylogenetic reconstruction: the propodeum with 4 or 5 pairs of lateral denticles and

the petiole dorsally armed. The combination of these two traits in characterising this clade is suggestive of what we understand as one of the major evolutionary trends in *Cephalotes*: improving its passive defence system (see chapter 6.7.3). All the members of the clade are South American, particularly abundant in the tropical zone, and extending up to Colombia as the northernmost limit.

Species included in the clade: *adolphi*, *angustus*, *conspersus*, *dentidorsum*, *frigidus*, *goeldii*, *notatus*, *pallidicephalus*, *palta*, *targionii*.

Cephalotes targionii (EMERY) new combination
Figs. 322, 323, 324, 325, 326

Cryptocerus targionii EMERY, 1894 a: 205. Soldier. Original description. Type locality: Mato Grosso. Type material: holotype soldier labelled "Mato Grosso, Germain" in MCSN (examined).

Cryptocerus denticulatus EMERY, 1894 a: 206. Worker. Original description. Type locality: Salinas on the Río Beni (Bolivia). Type material: 7 syntype workers (6 in MCSN, 1 in MHNG) partly labelled "Bolivia, Río Beni, Salinas, Balzan 1891", examined. Synonymy by KEMPF, 1958 a: 94.

Paracryptocerus targionii (EMERY), KEMPF, 1958 a: 94. Worker, soldier and gyne. First combination in *Paracryptocerus*.

Paracryptocerus conspersus (SMITH), KEMPF, 1958 b: 108 (partim). Nec SMITH, 1867. Misidentification.

D i a g n o s i s . - A member of the *angustus* clade differing, in the worker, from *conspersus* by the dark gaster instead of orange, and, from *palta*, by the narrower head; and, in the soldier, from *conspersus* and *palta* by the denser foveae on the floor of the cephalic disc.

W o r k e r (Fig. 322). - Head gently convex above, subquadrate. Frontal carinae diverging backwards, slightly converging in front and upturned above eyes. Vertexal angles truncate and with two pairs of small, obtuse, membranaceous denticles. Vertexal margin slightly concave and laterally connected with the internal pair of denticles through a thin carina. Clypeal suture little impressed. Mandibles with a thin, short lateral carina.

Mesosoma slightly convex. Scapular angles visible in dorsal view. Pronotal sides with three pairs of short, teeth, the first pair, triangular and separated from the second obtuse one by a superficial notch, the third pair broad, truncate, apically crenulate and separated from the two first pairs by a minute notch. Promesonotal suture vestigial or obsolete. Mesonotum with a pair of triangular teeth with obtuse or truncate tip. Propodeal suture more impressed on the sides. Propodeum slightly differentiated in basal and declivous face; declivous face little concave in the middle and as long as the basal one. Propodeal sides with 3 pairs of pointed teeth and with one to three additional pairs of denticles.

Petiole with sloping anterior face; its median dorsum with a pair of denticles. Sides of the petiole with a pointed, thin spine directed backwards. Postpetiole slightly broader than petiole; middle of the postpetiolar dorsum with a V-shaped carina; postpetiolar spines directed forwards at the base and curved at the apex.

Gaster oval. Anterolateral gastral border with a semitransparent lamella not surpassing the level of the stigma.

Hind femora without angle or denticle in the middle.

Sculpture. Head dorsum reticulate and covered by foveae as broad as their interspaces on the two anterior thirds, denser on the last third. Frontal carinae reticulate only. Ventral face of the head reticulate and with slightly impressed longitudinal rugulae. Trunk, posterior face of the petiole, and postpetiole with the same sculpture as on the posterior third of the head dorsum, more oval on the propodeum and less impressed on the pedicel. Middle of the declivous face of the propodeum, anterior face of the petiole, gaster and legs reticulate. Pleurae

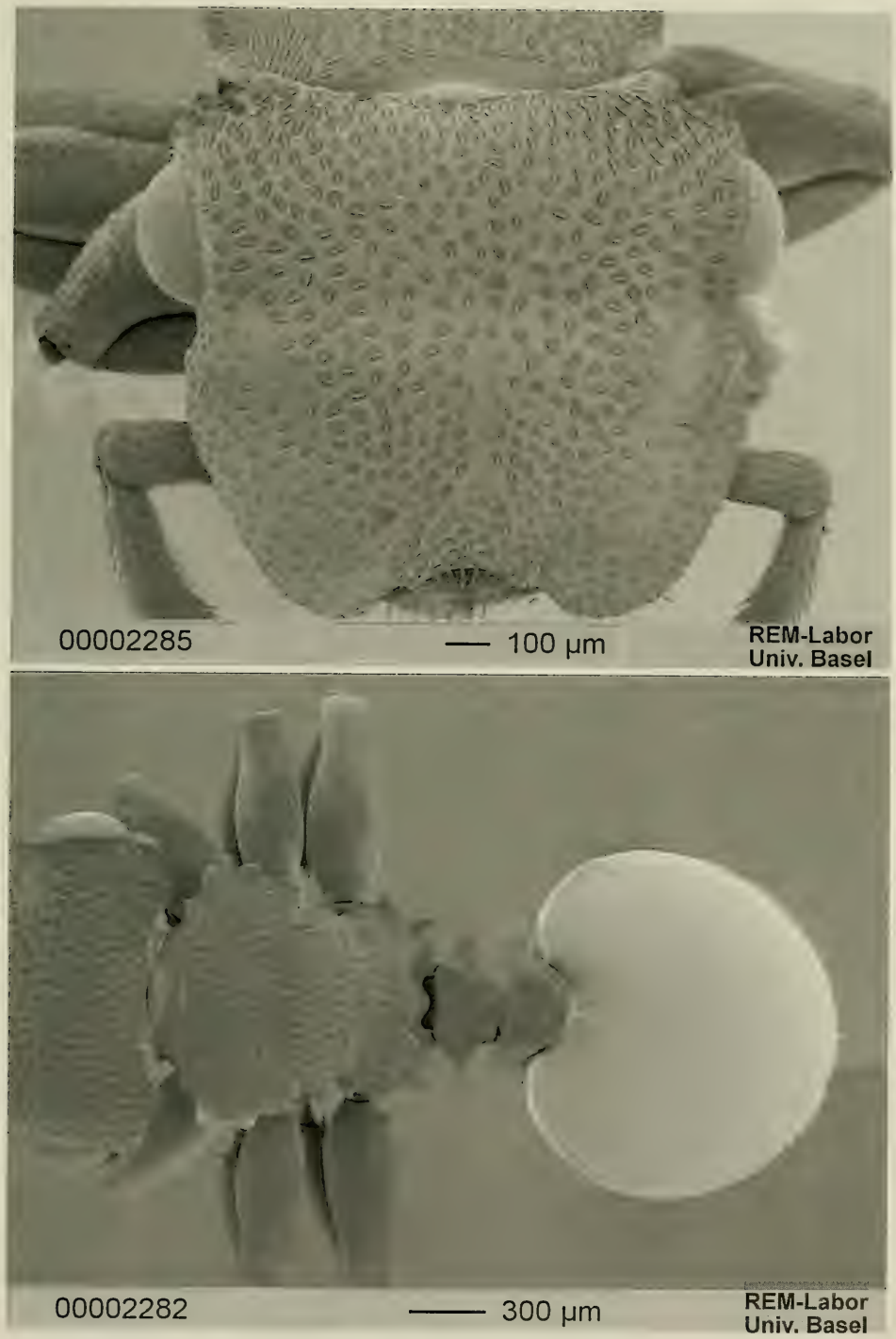


Fig. 322. *Cephalotes targionii* (EMERY). Worker from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

reticulate and longitudinally striate. First gastric tergite with superficial piligerous foveae. Center of the posterior half of the first gastral sternite shining.

Pilosity. Each fovea with an appressed canaliculate hair, slightly longer on the propodeum and on the pedicel. Mandibles, border of the frontal carinae and legs with sparse, suberect, canaliculate hairs. Legs and gaster with dense, appressed, canaliculate hairs as those on the propodeum, thinner on the gaster. Apex of the tergites and sternites with two types of erect hairs: (1) short, sparse and slightly canaliculate, (2) long, rare and pointed.

Colour. Body black. Frontal carinae, distal part of the scapes, first funicular joint, mesosomal and peduncular spines, anterolateral lamella of the gaster, apex of femora, outer face of the tibiae and tarsomeres yellowish to light ferrugineous. First gastral tergite black or with the following patterns of coloration: only the anterior fourth light brown, or anterior fourth and lateral borders light brown, or with a pair of dark yellow spots behind the lamellae.

Measurements (in mm) and indices: TL 3.88–4.70; HL 0.92–1.12; HW 1.08–1.28; EL 0.28–0.32; PW 0.88–1.04; PeW 0.52–0.57; PpW 0.55–0.65; HBaL 0.35–0.44; HBaW 0.09–0.11; CI 112.0–117.4; PI 119.1–123.1; PPeI 169.2–182.4; PPpI 160.0–164.9; HBaI 25.0–25.7.

S o l d i e r (Fig. 323). - Head with a complete disc, concave anteriorly and flat posteriorly. Sides of the head disc strongly converging before the beginning of the eyes and connected with the truncate posterior border of the disc. Lenght of the truncate border less than half of the maximum width of the head. Borders of the head disc strongly marginate and less raised posteriorly. Vertexal angles convex, obtuse and strongly marginate up to the posterior border of the eyes. Clypeal border concave and medially delimited by two denticles. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a thick carina ending in a small denticle just before the eyes. Eyes flat and not hidden by the head disc.

Mesosoma broad and almost flat in side view. Pronotum sloping; its anterior border convex mesially. Humeral angles obtuse. Pronotal sides convex. Pronotal carina thickening from the sides to the center where it is interrupted by a superficial sulcus. Promesonotal suture impressed. Mesonotum with a pair of broad, round tooth. Propodeal suture deeply impressed. Propodeum well differentiated in basal and declivous faces. Basal face medially as high as the mesonotum, laterally lower. Sides of the basal face of the propodeum with a small swelling followed by two pairs of teeth, the first pair short, broad and with almost round tip, the second one large, broad, thick, curved upwards and forwards at the apex and with obtuse tip. Declivous face concave in the middle; its sides converging posteriorly.

Petiole differentiated in anterior and posterior faces; anterior face sloping, separated from the short, declivous posterior face by a faint, transversal carina. Sides of the petiole with a pair of short, thick teeth directed backwards. Postpetiole convex and with a v-shape carina in the middle. Postpetiolar sides with a pair of thick spines arising from the anterior border and directed anterolaterally. Tip of the postpetiolar spines almost round.

Gaster oval, with a broad, protruding anterolateral lobe. Anterolateral border of the first gastral sternite with a very thin margin not reaching the stigma.

Hind femora without angle or denticle in the middle. Hind basitarsi slightly more compressed apically than distally, and without broad base.

Sculpture. Head dorsum reticulate and covered by large foveae broader than their interspaces, larger on the center of the head disc, shallower on the frontal carinae. Sides of the head superficially reticulate and with foveae one third of the size of those on the center of the disc, deeper posteriorly. Ventral part of the head deeply reticulate, its posterior half with larger, shallower and sparser foveae than on its anterior half. Mesosoma reticulate, with foveae almost as broad as those on the side of the head, the foveae are slightly larger and sparser on the pronotum, smaller, deeper and denser on the mesonotum and basal face of the propodeum. Declivous face of the propodeum reticulate and with faint, transversal rugosities. Pleurae reticulate; propleurae with longitudinal striae, this sculpture but less impressed and thinner on the lower metapleurae. Sparse foveae on the meso and metapleurae. Posterior face of the petiole and postpetiole with oval, superficial foveae. Anterior face of the petiole, gaster and legs reticulate. Disc of the posterior half of the first gastral sternite shining.

Fig. 323. *Cephalotes targionii* (EMERY). Soldier from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Pilosity. Each fovea with a subdecumbent or decumbent canaliculate hair, slightly longer and decumbent on the head disc. Legs and gaster with the same appressed hairs as on each fovea, thinner on the gaster. Mandibles and legs with rare, suberect, canaliculate hairs. Apex of the tergites and sternites with two types of erect hairs: (1) short, sparse and slightly canaliculate, (2) long, rare and pointed.

Colour. Ventral part of the head including the ventral third of its sides, clypeus, mesosoma, pedicel, coxae, femora and gaster dark brown to black. Head disc, the two dorsal thirds of the sides of the head, mandibles, sides of the pronotum, propodeal and pedicular spines, apex of femora, outer face of tibiae, tarsomeres and border of the tergites yellowish-orange to ferruginous, with darker antennae and basitarsi. Gaster with two pairs of yellow spots, the first pair anterolaterally, almost round and reaching the stigma, the second one oval and placed on the postero-lateral half of the gaster and not reaching the posterior border of the first gastric tergite. Body opaque to superficially shining.

Measurements (in mm) and indices: TL 5.16–7.08; HL 1.42–1.92; HW 1.42-.188; EL 0.32–0.37; PW 1.26–1.72; PeW 0.60–0.76; PpW 0.66–0.80; HBaL 0.38–0.47; HBaW 0.11–0.14; CI 95.7–100.0; PI 109.3–112.7; PPeI 210.0–228.2; PPpI 190.9–215.0; HBaI 28.9–29.8.

G y n e (Fig. 324). - Head with disc as in the soldier, but the floor of the disc less concave anteriorly and flat to gently convex posteriorly. Frontal carinae superficially crenulated. Ocelli placed far from the vertexal margin.

Mesosoma. Pronotum as in the soldier. Mesonotum and scutellum at the same plane and slightly flat. Propodeum well differentiated in basal and declivous faces. Basal face converging and with two pairs of teeth, the first pair short, broad and almost round and the second one longer and slightly directed laterally. Declivous face as in the soldier.

Petiole slightly square, with the anterior face sloping and with the posterior one short and flat. Petiolar sides with a short, pointed tooth. Postpetiole as in the soldier, but with the tip of its spines more pointed.

Gaster oval, narrow anteriorly, broadening posteriorly. Anterolateral gastral lobes protruding and with a thin margin not reaching the stigma.

Hind femora without angle or denticle in the middle. Hind basitarsi as in the soldier.

Wings as in Fig. 325.

Sculpture. Body integument as in the soldier, except for the mesonotum and scutellum with sparser foveae and for the upper mesopleurae densely foveolate.

Pilosity. As in the soldier, with the following differences: mesosoma and pedicel with the same rare, suberect, slightly clavate hairs as on the mandibles and legs; this same type of hairs surrounding the frontal carinae.

Colour. As in the soldier except for the center of the head disc light brown, and the dorsum of the pronotum with a yellow-orange triangle. Small specimens have the center of the disc completely black.

Measurements (in mm) and indices: TL 6.92–7.48 (dwarf specimen 5.84); HL 1.48–1.68 (dwarf specimen 1.24); HW 1.44–1.64 (dwarf specimen 1.28); EL 0.37–0.38 (dwarf specimen 0.34); PW 1.38–1.56 (dwarf specimen 1.20); PeW 0.57–0.60 (dwarf specimen 0.53); PpW 0.75–0.76 (dwarf specimen 0.63); HBaL 0.48–0.51 (dwarf specimen 0.47); HBaW 0.14–0.15 (dwarf specimen 0.12); CI 97.3–97.6 (dwarf specimen 103.2); PI 104.3–105.1 (dwarf specimen 106.7); PPeI 242.1–260.0 (dwarf specimen 226.4); PPpI 184.0–205.2 (dwarf specimen 190.5); HBaI 29.2–29.4 (dwarf specimen 25.5).

M a l e (previously undescribed). - Head (eyes included, mandibles excluded) about 1/3 broader than long. Vertexal angles gently convex and without median angles. Ocelli protuberant. Vertex moderately convex. Frontal carinae simply marginate, diverging backwards and not reaching the posterior border of the eyes. Frons superficially concave medially. Clypeus convex. Mandibles short and laterally carinate. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma robust. Anterior pronotal border convex. Pronotal sides in dorsal view subparallel and slightly marginate in few specimens only. Mayrian furrows impressed; parapsidal furrows variably impressed. Propodeal sides converging posteriorly.

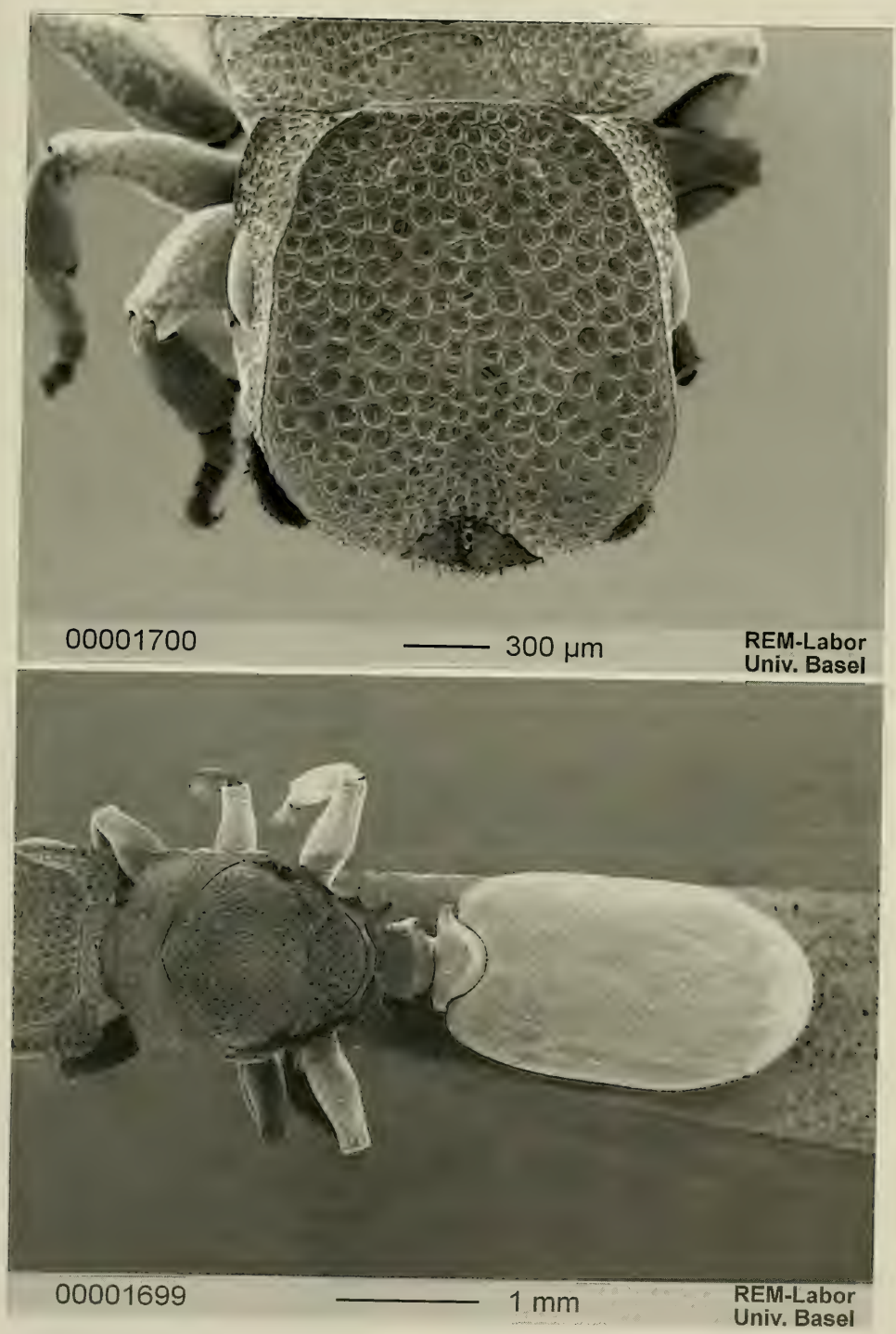


Fig. 324. *Cephalotes targionii* (EMERY). Gyne from Lins (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

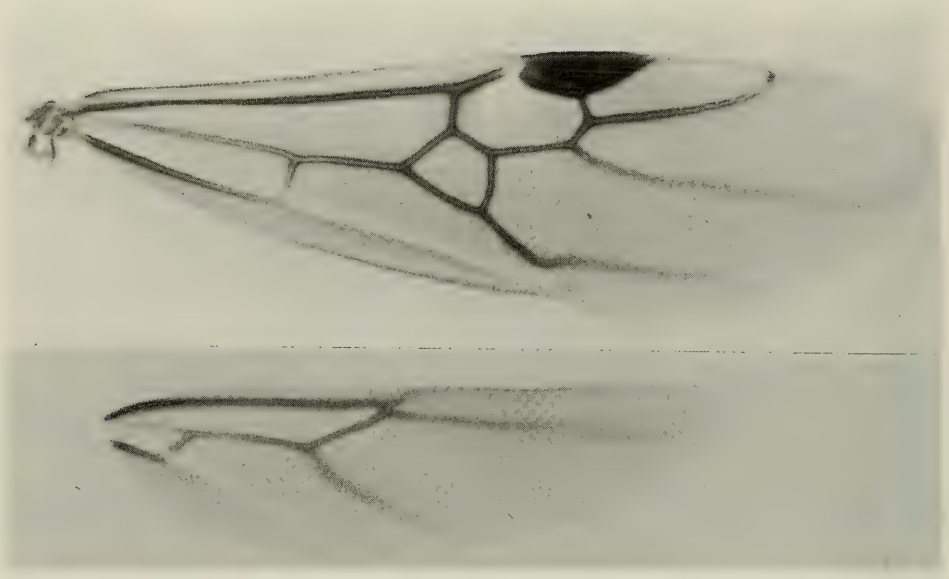


Fig. 325. *Cephalotes targionii* (EMERY). Gyne from Lins (São Paulo), Brazil, fore and hind wings.

Petiole narrower than the postpetiole and with truncate and medially concave anterior face; petiolar sides convex anteriorly and converging posteriorly. Postpetiolar dorsum convex; postpetiolar sides subconvex, sometimes with a minute, round denticle.

Gaster almost as broad as the mesosoma.

Genitalia and subgenital plate as in Fig. 326.

Sculpture. Body shining, head subopaque. Head dorsum minutely punctate and irregularly foveolate rugose, the rugosities slightly transversal around the eyes. Ventral part of the head with the same type of sculpture as on the posterior part of the dorsum but with more irregular foveae and with transversal rugosities around the eyes. Pronotum superficially punctate and foveolate. Mesonotum and scutellum sparsely punctate and foveolate, the foveae very small and superficial. Basal face of the propodeum with dense, thick, longitudinal rugosities. Pleurae variably punctate-foveolate and with thin, longitudinal rugosities. Pedicel, gaster, coxae and femora with traces of superficial reticulation. Tibiae and tarsi punctate.

Pilosity. Body with long, erect, pointed hairs, denser on the head and on the mesosoma, rare on the first gastral tergite, appressed on the posterior border of the gastral tergites and absent on the tibiae and tarsi. Gaster, tibiae and tarsi with short, appressed hairs, denser on the tibiae and tarsi.

Colour. Head, mesosoma, pedicel and coxae black. Gaster brown. Femora lighter. Remaining parts of the legs yellowish.

Measurements (in mm) and indices: TL 5.20–5.80; HL 0.76–0.78; HW 0.96–1.02; EL 0.38–0.40; PW 1.00–1.04; PeW 0.36–0.39; PpW 0.43–0.44; HBaL 0.61; HBaW 0.08; CI 126.3–130.8; PI 92.3–102.0; PPeI 226.7–277.8, PPpI 227.3–241.8; HBaI 13.1.

Material examined: **Venezuela**: no further locality, 03.X.1941, intercepted in Hoboken (New Jersey), in *Cattleya* pseudobulb, 4 workers [USNM]; no further locality, II.IV.1941, intercepted in Hoboken (New Jersey), in *Cattleya*, 4 workers, 3 soldiers, 3 males [MZSP, USNM]. Distrito Federal: Caracas, 24.VIII.1940, intercepted in Hoboken (New Jersey), in *Cattleya*, 3 workers [USNM]; same locality, 29.III.1946, intercepted in San Francisco, 5 workers, 2 soldiers, 3 males [MZSP, USNM]. Zulia: 31 km SW of Machiques, 14.IV.1981, 1 gyne, E. E. GRISSELL [USNM].

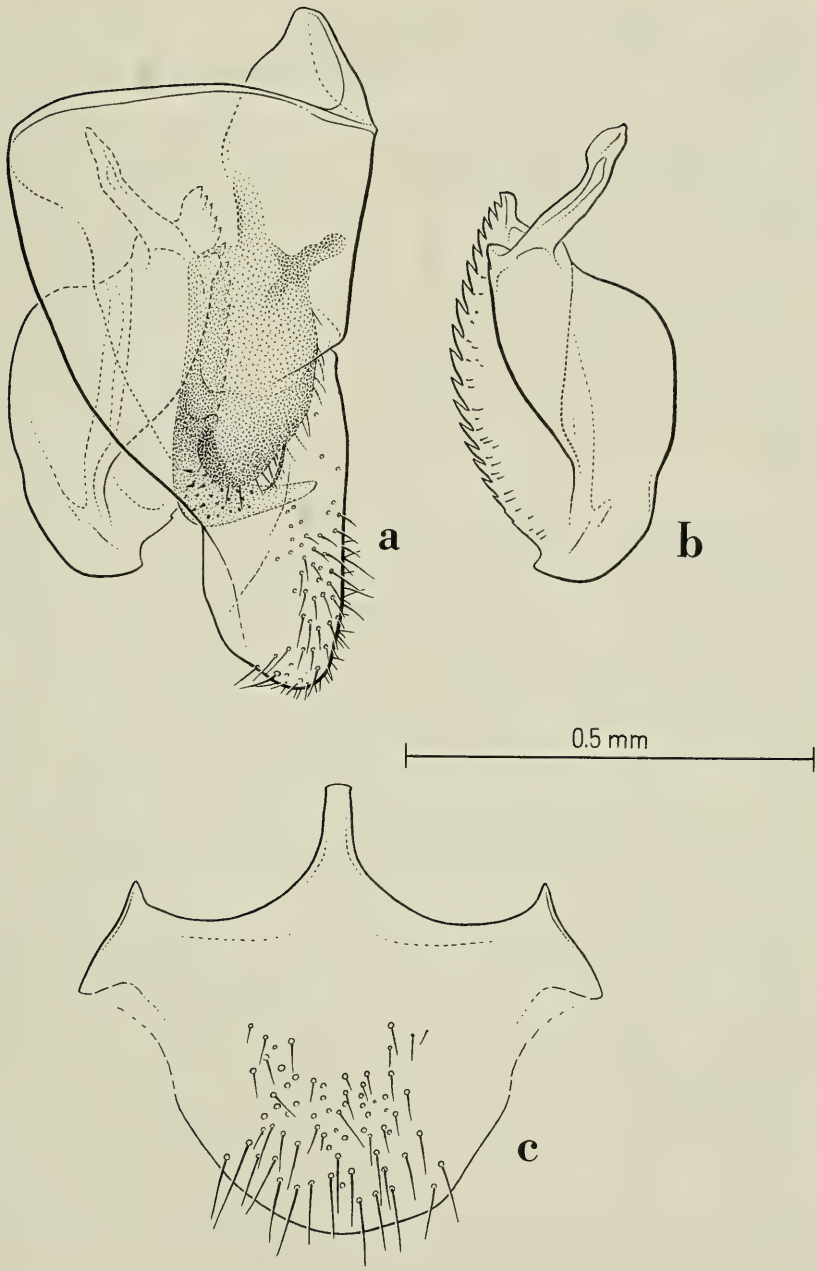


Fig. 326. *Cephalotes targionii* (EMERY). Male from Lins (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Trinidad & Tobago: Trinidad: St. Augustine, 1 gyne (without gaster), DARLINGTON [MZSP]; same locality, 28.XI.1934, 1 worker, 2 soldiers, 1 gyne, N. A. WEBER [MCZC].

Guyana: Forest Settlement, R. Mazaruni, VIII.1935, 1 worker, 1 soldier, N. A. WEBER [MCZC].

Brazil: Mato Grosso: no further locality, 1 soldier (holotype of *targionii*), GERMAIN [MCSN]; Chapada dos Guimarães, 30.1.1961, 1 gyne, J. &. B. BECHYNÉ; Chapada dos Guimarães, Fazenda Buriti, 9–14.2.1985, 1 worker, C. R. F. BRANDÃO & F. CAETANO [MZSP]. São Paulo: Agudos, 02.X.1953, 3 workers, W. W. KEMPF [MCZC, MZSP]; Boracéia, Itapuí, VII.1960, 1 worker, R. MUELLER [MZSP]; Anhembi, Fazenda B. Rico, 14.II.1969, 1 worker, J. C. MAGALHÃES et al. [MZSP]; Bôa Esperança do Sul, Fazenda Itaquerê, 21.VII.1964, 21.VII.1965, 16 workers, 4 soldiers, K. LENKO [MZSP]; Nova Europa, Fazenda Itaquerê, 24.VIII.1963, 1 worker, K. LENKO [MZSP]; Mococa, 15.8.1990, 1 worker, M. L. DE ANDRADE [NHMB]; Lins, 06.IX.1995, 24 workers, 15 soldiers, 8 gynes, 4 males, M. L. DE ANDRADE [CPCC, ZSMC, LACM, MCZC, NHMB].

Bolivia: Beni: Salinas, south of Río Beni, 1891, 7 workers (all syntypes of *denticulatus*), BALZAN [MCSN, MHNG].

Paraguay: La Cordillera: San Bernardino, 1 worker, 1 soldier, 1 gyne, K. FIEBRIG [ZSMC].

Discussion. - There is no doubt that *C. denticulatus* described by EMERY (1894 a: 206) from workers from Bolivia is the worker of *targionii* EMERY (1894 a: 205) described on a single soldier from Mato Grosso. The synonymy of *denticulatus* with *targionii* proposed by KEMPF (1958 a) without examining the type material is here confirmed by our examination of the types. In the same paper, KEMPF synonymised with *targionii* also *denticulatus* var. *variegata* FOREL from Amazonas, without seeing the type material. Our study of the syntypes of the var. *variegata* convinced us that this is a junior synonym of *conspersus*. In a subsequent paper, KEMPF (1958 b) after examining the type of *conspersus* (SMITH, 1867; a worker), considered it so similar to *targionii* as to regard *conspersus* as a senior synonym of the latter. His reasoning was based on the fact that the type of *conspersus* fits exactly the description of the var. *variegata*, and, on this basis, he decided the synonymy between *targionii* and *conspersus*. As we already said, we confirm the synonymy between *conspersus* and the var. *variegata*. But our study of the types of all the taxa involved shows that *targionii* cannot be considered a synonym of *conspersus*. The two species differ in microsculpture and coloration as already stated in the diagnosis. These differences hold for all the 125 female specimens of the three castes of *targionii* and for the 11 *conspersus* we examined.

The sole available worker from Guyana differs from the other examined in having a narrower gaster.

We collected and kept in the laboratory a part of a colony from Lins (S. Paulo) with two well differentiated types of gynes: the larger ones had orange head with a brown spot on the frons and the small ones had largely black head. The measurements of one of these dwarf gynes are reported in parentheses after the measurements of the "normal" ones. Our laboratory observations did not reveal behavioural differences among the two types of unfertilised gynes. We have circumstantial evidence that a similar gyne dimorphism should be present also among other *Cephalotes* species (*depressus*, *jheringi*) but we did not discuss these cases under the proper species since we have no unequivocal proof that gynes of different sizes originate from the same nest.

Distribution: Venezuela, Trinidad, Guyana, Brazil, Bolivia, Paraguay.

Cephalotes palta DE ANDRADE new species
Figs. 327, 328

Cryptocerus denticulatus EMERY, FOREL, 1912: 199. Worker. Nec EMERY, 1894 a. Misidentification.

Type material: holotype worker from Colombia, Santa Marta, FOREL, in MHNG; paratype, one worker, same data and collection as the holotype in MHNG.

Derivatio nominis: This species is named after the Palta, one of the ancient peoples of Colombia.

Diagnosis. - A member of the *angustus* clade differing from its sister species, *conspersus*, in the worker by the unicolourous first gastral tergite and, in the soldier, by the denser and smaller foveae on the disc.

Worker (Fig. 327). - Head convex above, subquadrate. Frontal carinae diverging backwards, slightly converging in front and little upturned above eyes. Vertexal angles truncate and with two pairs of obtuse, membranaceous projections. Vertexal margin slightly concave and laterally connected with the internal pair of denticles through a thin carina. Clypeal suture impressed. Mandibles with a thin, short lateral carina.

Mesosoma convex in side view. Scapular angle visible in dorsal view. Pronotal sides with three pairs of short, membranaceous teeth, the first pair, triangular and separated from the second almost truncate one by a superficial notch on the pronotal membrane, the third pair broad, truncate and separated from the two first pairs by a deep notch. Promesonotal suture vestigial. Mesonotum with a pair of triangular teeth with pointed tip. Propodeal suture more impressed on the sides. Propodeum slightly differentiated in basal and declivous face; declivous face little concave in the middle and shorter than the basal one. Propodeal sides with four to six pairs of pointed denticles, sometimes the first, third, fifth and sixth pairs thinner and much smaller than the second and fourth pairs.

Petiole with oblique anterior face; its median dorsum with a pair of denticles on the short posterior face. Sides of the petiole with a pointed, thin spine slightly curved. Postpetiole slightly broader than petiole; middle of the postpetiolar dorsum with a V-shaped carina; postpetiolar spines directed forwards at the base and curved at the apex.

Gaster oval. Anterolateral border of the gaster with semitrasparent lamella not surpassing the level of the stigma.

Hind femora without angle or denticle in the middle.

Sculpture. Head dorsum minutely reticulate and covered by foveae as broad as their interspaces on the two anterior thirds, denser on the last third. Frontal carinae reticulate and superficially foveolate. Ventral face of the head reticulate and with slightly impressed longitudinal rugulae close to the hypostoma. Trunk, petiole, and postpetiole with the same sculpture as on the posterior third of the head dorsum, more round on the center of the trunk and less impressed on the pedicel. Middle of the declivous face of the propodeum, anterior face of the petiole, gaster and legs reticulate. Pleurae reticulate and longitudinally striate. Gaster with superficial piligerous foveae, less impressed on the sternites. Disc of the posterior half of the first gastral sternite shining.

Pilosity. Each fovea with an appressed canaliculate hair. Mandibles, border of the frontal carinae and legs with sparse, suberect, canaliculate hairs. Extensor face of the legs and gaster with appressed canaliculate hairs slightly thinner on the gaster. Apex of the tergites and sternites with two types of erect hairs: (1) short, sparse and slightly canaliculate, (2) long, rare and pointed.

Colour. Black. Frontal carinae, distal part of the scapes, basal and distal part of the funiculus, thoracic and peduncular spines, anterolateral lamellae of the gaster, apex of femora, outer face of the tibiae and tarsomeres yellowish-orange to light ferruginous.

Measurements (in mm) and indices: TL 4.46–4.62; HL 1.04; HW 1.28–1.34; EL 0.32–0.33; PW 1.12–1.18; PeW 0.59–0.61; PpW 0.63; HBaL 0.37–0.44; HBaW 0.11–0.12; CI 123.1–128.8; PI 113.5–114.3; PPeI 183.6–200.0; PPpI 177.8–187.3; HBaI 27.3–29.7.

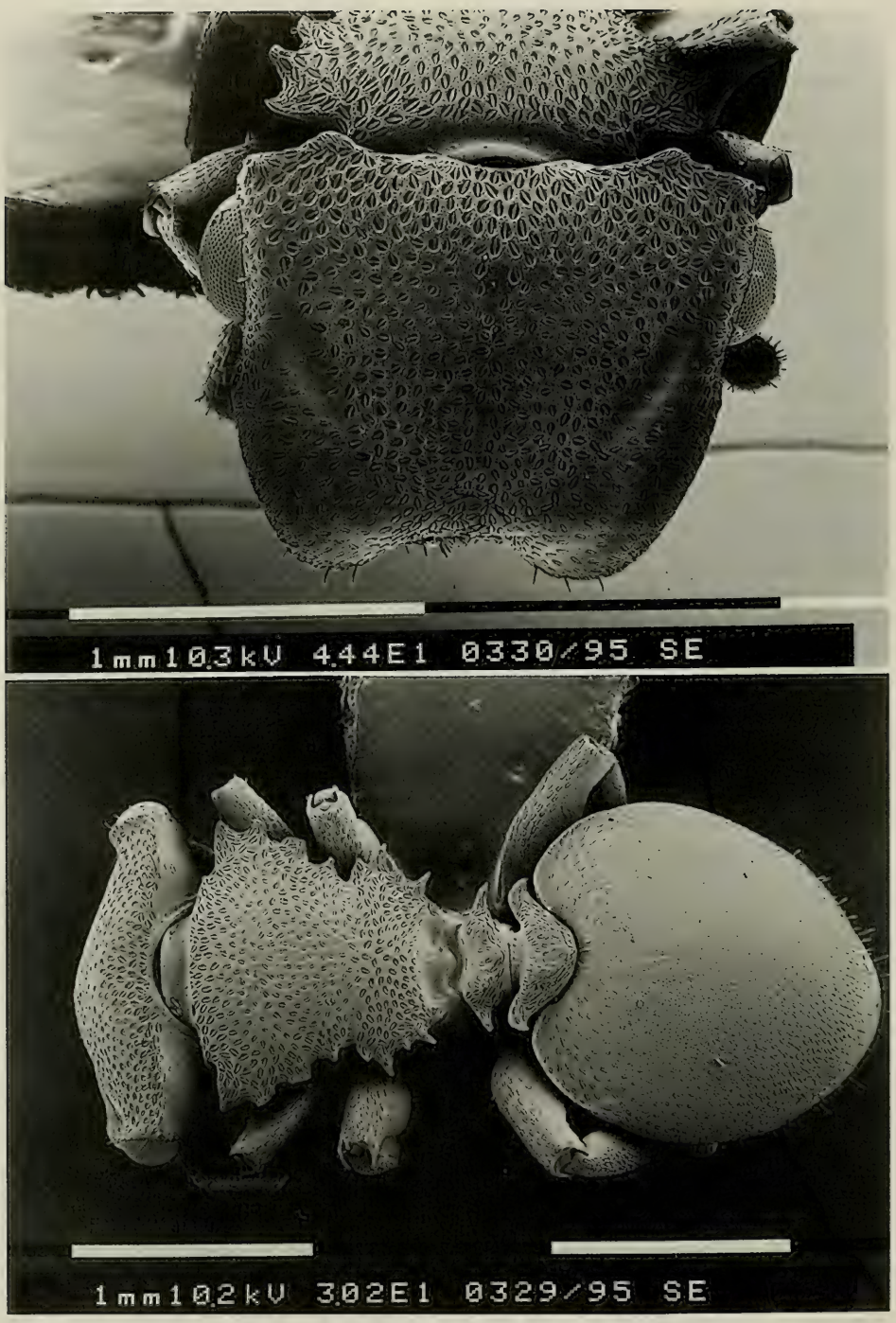


Fig. 327. *Cephalotes palta* DE ANDRADE. Worker from Río Frío (Magdalena), Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

S o l d i e r (Fig. 328). - Head with a complete disc, concave anteriorly and flat posteriorly. Sides of the head disc gently converging before the beginning of the eyes and connected with the posterior border of the disc. Borders of the head disc strongly marginate and weakly raised posteriorly. Vertexal angles much lower than the disc, convex, with a median denticle and marginate up to the anterior part eyes. Clypeal border concave and medially delimited by two denticles. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a carina ending in an obtuse denticle just before the eyes. Eyes flat and partially hidden by the head disc.

Mesosoma broad and almost flat in side view. Humeral angles obtuse. Anterior half of the pronotum sloping anteriorly; its anterior border convex mesially. Pronotal sides marginate and slightly converging posteriorly. Pronotal carina thickening from the sides to the center where it is interrupted by a superficial sulcus. Promesonotal suture more impressed on the sides. Mesonotum with a pair of broad, round expansion. Propodeal suture deeply impressed. Propodeum well differentiated in basal and declivous faces. Basal face medially as high as the mesonotum, laterally lower. Sides of the basal face of the propodeum with two pairs of teeth, the first pair short, broad and with almost round tip, the second one large, broad, thick, curved upwards and forwards at the apex and with obtuse tip. Declivous face concave in the middle; its sides converging posteriorly.

Petiole differentiated in anterior and posterior faces; anterior face oblique, almost truncate, separated from the short, declivous posterior face by an incomplete transversal carina. Sides of the petiole with a pair of short, thick teeth slightly curved backwards. Postpetiole convex and with a U-shaped carina in the middle of the dorsum. Postpetiolar sides with a pair of thick teeth arising from the anterior border and directed anterolaterally. Tip of the postpetiolar spines almost round.

Gaster oval, with a broad, protruding, anterolateral lobe. Anterolateral border of the first gastral tergite with a thin margin not reaching the stigma.

Hind femora without angle or denticle in the middle. Hind basitarsi slightly more compressed apically than distally, and without broad base.

Sculpture. Head dorsum minutely reticulate and covered by small foveae slightly broader than their interspaces, shallower and smaller on the frontal carinae. Sides of the head superficially reticulate and with foveae half of the size of those on the disc, deeper on the posterior half. Ventral part of the head reticulate-foveolate anteriorly, this sculpture becomes less impressed and shining posteriorly. Mesosoma reticulate, with foveae almost as broad as those on the side of the head, the foveae are slightly larger and sparse on the pronotum, smaller, on the mesonotum and on the basal face of the propodeum. Declivous face of the propodeum reticulate and with faint, transversal rugosities on the middle. Pleurae reticulate; propleurae with nearly longitudinal striae, this same sculpture but less regular and faint on the lower metapleurae. Sparse foveae on the meso and metapleurae. Posterior face of the petiole, postpetiole with oval and superficial foveae. Anterior face of the petiole, gaster and legs reticulate. Extensor face of the legs and anterior fourth of the first gastral tergite with superficial, oval foveae. Disc of the posterior half of the first gastral sternite shining.

Pilosity. Each fovea with an appressed canaliculate hair. Legs and gaster with the same appressed hairs as on each fovea, thinner on the gaster. Mandibles, anterior border of the head disc, mesosoma, pedicel, legs and gaster with rare, suberect, subclavate hairs. Apex of the tergites and sternites with two types of erect hairs: (1) short, sparse and slightly canaliculate, (2) long, rare and pointed.

Colour. Ventral part of the head including the ventral third of its sides, clypeus, thorax, pedicel, coxae, femora and gaster black. Head dorsum, including the two dorsal thirds of the sides of the head, mandibles, sides of the pronotum, of the propodeum and of the pedicellar spines, apex of femora, outer face of tibiae and tarsomeres yellowish-orange, with darker antennae and basitarsi. Gaster with two pairs of yellow spots, the first pair anterolaterally, the second one placed on the postero-lateral half of the gaster.

Measurements (in mm) and indices: TL 6.40; HL 1.76; HW 1.76; EL 0.36; PW 1.64; PeW 0.61; PpW 0.67; HBaL 0.43; HBaW 0.14; CI 100.0; PI 117.3; PPeI 268.8; PPpI 244.8; HBaI 32.6.

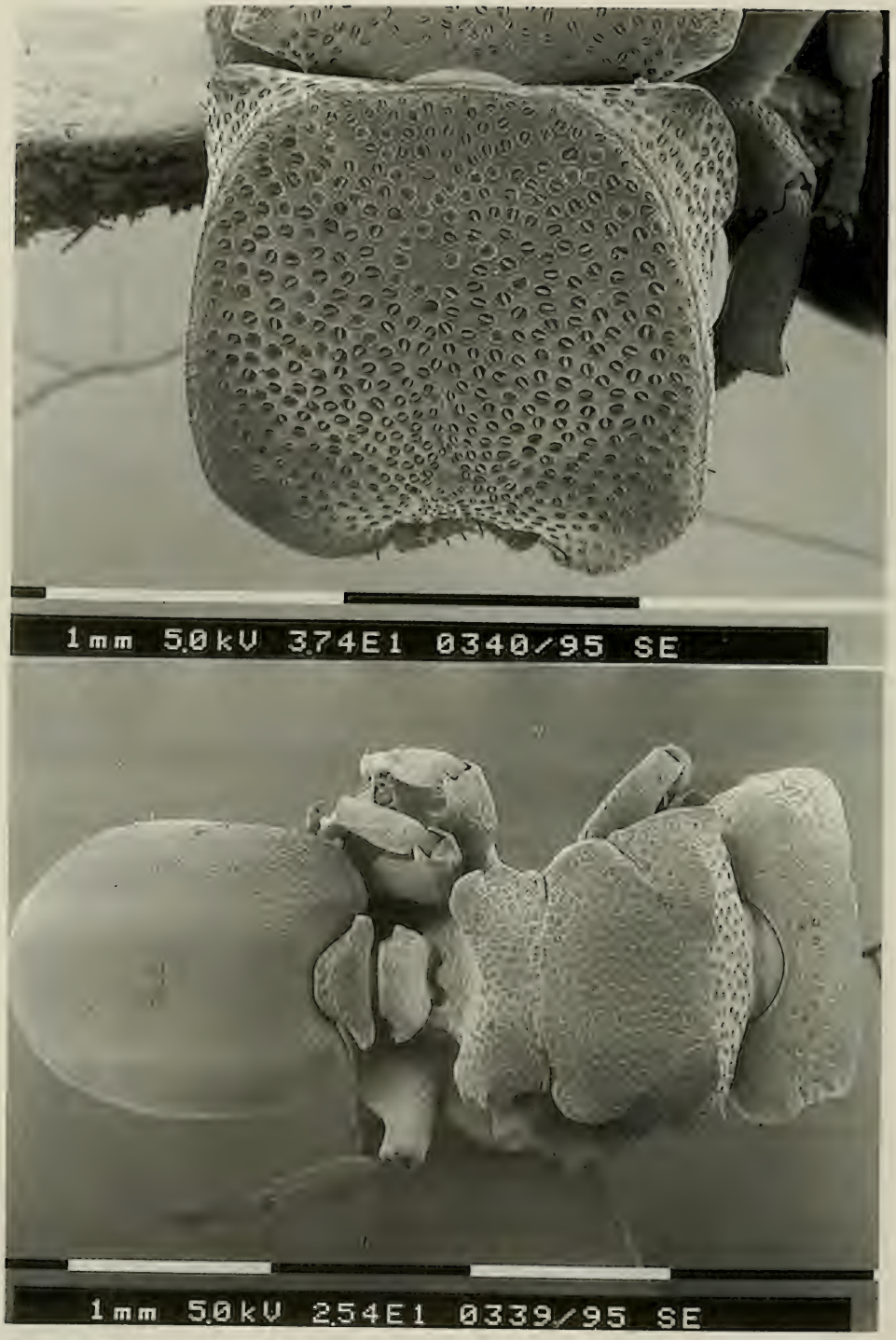


Fig. 328. *Cephalotes palta* DE ANDRADE. Soldier from Río Frío (Magdalena), Colombia: head (top) and meso- and metasoma (bottom) in dorsal view.

Material examined. – **Colombia**: Magdalena: Santa Marta, 2 workers (holotype and paratype), FOREL [MHNG]; Río Frío, 26.II.1928, 1 worker, 1 soldier, DARLINGTON [MCZC].

Discussion. - *C. palta* is similar to *conspersus*, but the two can be distinguished, in addition to the characters already cited in the diagnosis, in the worker, by the pronotal width greater than the head length in *palta* vs. smaller in *conspersus*; by the petiolar dorsum with salient denticles in *palta* vs. minute in *conspersus*; by the postpetiole with a U-shaped carina in *palta* vs. simply convex in *conspersus*; by the gaster unicolourous in *palta* vs. bicoloured in *conspersus*.

Distribution: Colombia.

Cephalotes conspersus (SMITH) new combination
Fig. 329

Cryptocerus conspersus SMITH, 1867: 253, pl. 26, fig. 1. Worker. Original description. Type locality: Rio Amazonas, Brazil. Type material: holotype, unique, worker labelled "121, Type, Amaz, *Cryptocerus conspersus*. Sm. Trans Ent. Soc., *Cryptocerus conspersus* Sm. 1867 Holotypus, *Paracryptocerus conspersus* (F. Sm.) 1867 det. Kempf 1957, Type Hym. 1045", in OXUM, examined. KEMPF, 1958 b.

Cryptocerus denticulatus var. *variegata* FOREL, 1911: 262. Worker. Original description. Type locality: Amazonas. Type material: 3 syntype workers labelled "Amazonas, H. W. Bates S.", 1 in MHNG, 2 in ZSMC, examined. Synonymy with *targionii* by KEMPF, 1958 a: 94. Synonymy with *conspersus* by KEMPF, 1958 b: 108. Confirmed by our examination of the type material of both taxa.

Paracryptocerus conspersus (SMITH), KEMPF, 1951: 232. First combination in *Paracryptocerus*.

Paracryptocerus conspersus (SMITH), KEMPF, 1958 b: 108. Worker.

Zacryptocerus conspersus (SMITH), BRANDÃO, 1991: 385. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *angustus* clade differing from its sister species, *palta*, in the worker by the first gastral tergite bicoloured and, in the soldier, by the foveae on the disc sparser and larger.

Worker (Fig. 329). - Head convex above, subquadrate. Frontal carinae superficially crenulate, diverging backwards, slightly converging in front, little upturned above the eyes. Vertexal angles truncate, bearing a pair of small, obtuse, membranaceous denticles, often with a minute notch in the middle. Vertexal margin concave and laterally connected to the denticles by means of a thin carina. Clypeal suture superficially impressed. Mandibles with a faint, thin, short, lateral carina.

Mesosoma gently convex. Scapular angles free. Pronotal sides with three pairs of short, membranaceous teeth, the first and the second pair triangular, the third pair, broader than the others, obtuse. Promesonotal suture poorly impressed. Mesonotum with a pair of triangular denticles with truncate tip. Propodeal suture more impressed on the sides. Propodeum with poorly differentiate basal and declivous faces; declivous face concave in the middle and shorter than the basal one. Propodeal sides with five, rarely six pairs of pointed denticles, sometimes the first, third, fifth and sixth pairs thinner and much smaller than the second and fourth pairs.

Petiole with truncate anterior face; its posterior face sloping and separate from the anterior one by a pair of minute denticles. Sides of the petiole with a pair of pointed, thin spines directed slightly backwards. Postpetiole convex and as broad as the petiole; postpetiolar spines directed slightly forwards at the base and curved at the apex.

Gaster oval. Anterolateral gastral border with semitransparent lamella reaching the stigma. Hind femora subangulate to angulate.

Sculpture. Head dorsum reticulate and covered by superficial foveae as broad as their interspaces and slightly denser on the vertexal angles. Frontal carinae reticulate only. Ventral face of the head reticulate and with few, faint, longitudinal rugulae close to the hypostoma. Mesosoma, posterior face of the petiole, and postpetiole with the same sculpture as on the vertexal angles, the foveae more oval on the propodeum and less impressed on the pedicel. Middle of the declivous face of the propodeum, anterior face of the petiole, gaster and legs simply reticulate. Pleurae reticulate and with superficial, longitudinal striae. First gastral sternite with superficial, oval piligerous punctures. Middle of the posterior half of the first gastral sternite shining.

Pilosity. Each fovea with an appressed canaliculate hair, both slightly longer on the propodeum and on the pedicel. Mandibles, border of the frontal carinae and legs with sparse, suberect hairs. Extensor face of the legs and gaster with dense, appressed hairs as those on the propodeum, thinner on the gaster. Posterior borders of the gastral tergites with clavate hairs; gastral sternites with the same clavate hairs as the tergites and rare, long and pointed hairs.

Colour. Black. Frontal carinae, distal part of the scapes, three first funicular joints, thoracic and peduncular spines, distal half of the femora, tibiae and tarsomeres yellowish to ferruginous. First gastral tergite with the following black parts: a pair of oval anterolateral spots and a lozenge in the middle, the rest ferruginous.

Measurements (in mm) and indices: TL 3.46–3.92; HL 0.88–0.94; HW 0.96–1.08; EL 0.28–0.30; PW 0.76–0.88; PeW 0.50–0.54; PpW 0.50–0.54; HBaL 0.35–0.37; HBaW 0.07; CI 109.1–114.9; PI 122.7–126.3; PPeI 152.0–162.9; PPpI 152.0–162.9; HBaI 18.9–20.0.

S o l d i e r (previously undescribed and tentative attribution). - Very similar to that of *palta* from which it differs in the following details: Floor of the disc less concave anteriorly. Humeral angles pointed. Pronotal sides subparallel. Pronotal carina superficially marked. Promesonotal suture impressed. Propodeum with well differentiate basal and declivous faces. Sides of the basal face anteriorly with three denticles, the first denticle smaller the others and the third one curved upwards. Declivous face concave in the middle; its sides converging posteriorly and bearing a minute denticle. Postpetiole more convex and with the "U" shaped carina less marked. Gastral lobes more oval. Anterolateral border of the first gastral sternite with a very thin margin not reaching the stigma posteriorly. Fore femora slightly incrassate. Hind femora without angles or denticles. Hind basitarsi slightly more compressed apically than distally and without broad base. Hind femora subangulate.

Sculpture. Foveae on the head larger and sparser on the dorsum, shallower on the ventral part. Propleurae with longitudinal striae on the lower part. Anterior fourth of the first gastral tergite with sparser foveae.

Pilosity. Mesosoma and pedicel without subclavate hairs.

Colour. Ventral part of the head including half of its sides, mesosoma, pedicel, coxae, femora, mid and hind tarsi and gaster black. Head dorsum, including the dorsal half of the sides, apex of femora, fore tibiae and fore tarsi, outer face of mid and hind tibiae, and tarsomeres yellowish-orange. Gaster with two pairs of yellow spots on the first tergite, the first pair anterolaterally, the second one placed on the postero-lateral half of the gaster.

Measurements (in mm) and indices: TL 4.92; HL 1.40; HW 1.32; EL 0.32; PW 1.16 PeW 0.56; PpW 0.59; HBaL 0.36; HBaW 0.10; CI 94.3; PI 113.8; PPeI 207.1; PPpI 196.6; HBaI 27.8.

M a t e r i a l e x a m i n e d. – **Brazil**: A m a p á : Highway BR. 156, km 14, 30.XI.1981, 1 worker, Gorayeb [MPEG]. A m a z o n a s : no further locality, 1 worker (holotype of *conspersus*) [OXUM]; no further locality 3 workers (syntypes of *denticulatus* var. *variegata*), H. W. Bates S. [MHNG, ZSMC]; Manaus, Reserva Flor. A. Ducke, 2° 55' S, 59° 59' W, terra firme, 21.II.1992, 1 worker, J. Adis et al. [INPA]. R o n d ô n i a : Vilhena, XI.1973, 1 worker, M. Alvarenga [MZSP]. G o i á s : Jataí, XI.1972, 1 soldier, F. M. Oliveira [MZSP]. M a t o G r o s s o : Mato Grosso, 28.VII.1972, 1 worker, R. N.

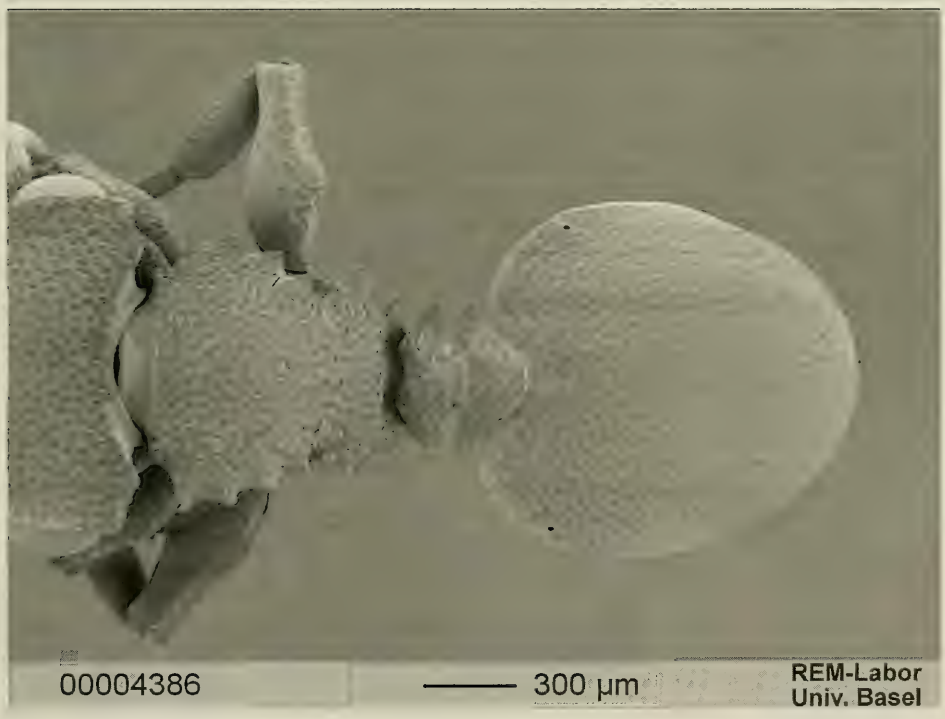


Fig. 329. *Cephalotes conspersus* (SMITH). Worker from Vilhena (Rondônia), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

WILLIAMS [MZSP]; Vila Vera, X.1973, 1 worker, M. ALVARENGA [MZSP]. Mato Grosso do Sul: Jardim, I.1962, 1 worker, R. MÜLLER [MZSP].

Discussion. - *C. conspersus* is easily distinguished from *palta* and from *targionii* by the gastral coloration. KEMPF (1958 b) after examining the type of *conspersus* considered the characters used to separate it from *targionii* as unimportant since they were probably correlated with the smaller size of the *conspersus* type. We examined large series of *targionii* and 10 workers of *conspersus* and the minute morphological differences listed by KEMPF (l. c.) appear to be constant among all the specimens. In addition to the characters already discussed by KEMPF (l. c.), the integumental sculpture of *conspersus* is much more superficial than that of *targionii*. We agree with KEMPF (1958 b) in considering *denticulatus* var. *variegata* FOREL as a synonym of *conspersus*. Actually, the two are probably based on different specimens from the same series.

The workers of *conspersus*, in general, have the mid and hind femora very weakly angulate, but one specimen has clearly angulate femora. This is the sole occurrence of angulate femora within the *angustus* clade.

We tentatively attribute the isolated soldier from Jatai (a small specimen) to *conspersus*. This soldier is quite similar to that of *palta*, the sister species of *conspersus*, and differs from it by the same sculptural characters separating the workers of the two species and, additionally, by the subangulate hind femora.

FERNÁNDEZ et al. (1996) report this species from the Colombian state of Meta. We saw no Colombian specimens referable to this species. Although the record from Colombia is plausible, there is a chance that the specimens in question may refer to the closely related *palta* described from Colombia in this paper.

Distribution: Brazil.

Cephalotes angustus (MAYR)

Figs. 330, 331, 332, 333, 373, 374, 375

Cryptocerus angustus MAYR, 1862: 759. Worker and gyne. Original description. Type locality: Brazil. Type material: not available in the MAYR collection in the NHMW; as already noted by KEMPF (1958 a) a series of 2 soldiers, 2 workers and 1 male from Santa Catharina in NHMW, labelled as types and collected by HEČKO cannot represent the true types. We regard as probable syntypes 2 workers and 1 soldier labelled „C. *angustus* Mayr, Brésil, cotypus", in MHNG.

Cryptocerus angustus MAYR, MAYR, 1887: 565. Male.

Cryptocerus angustus var. *clarior* FOREL, 1912: 201. Worker. Original description. Type locality Rio de Janeiro. Type material 9 syntype workers partly labelled "*Cr. angustus* Mayr v. *clarior* For. type, Rio, Göldi III,", and partly "Prov. Rio, Göldi, III, *Cr. angustus* Mayr var. *clarior* Forel" in MHNG and NHMB, examined. One specimen without head and gaster in MHNG selected as lectotype by KEMPF (1951) according to the label. Synonymy by KEMPF, 1958 a: 74.

Cryptocerus cristatus var. *ruficeps* SANTSCHI, 1929: 301. Worker. Original description. Type locality: Brazil. Type material: holotype, unique in NHMB with two labels; first label: "Bresil, K. Zubac" (sic); second label: "*Cryptocerus angustus* Mayr v. *ruficeps* (cancelled) Santschi det. 19 (printed) 4", examined.

Paracryptocerus ?cristatus (EMERY), KEMPF, 1951: 216 (partim, see under *cristatus*).

Paracryptocerus angustus (MAYR), KEMPF, 1958 a: 20, 74, pl. 1, figs. 2, 4, 7; pl. 3, figs. 2, 5; pl. 6, fig. 5. Worker, soldier. First combination in *Paracryptocerus*.

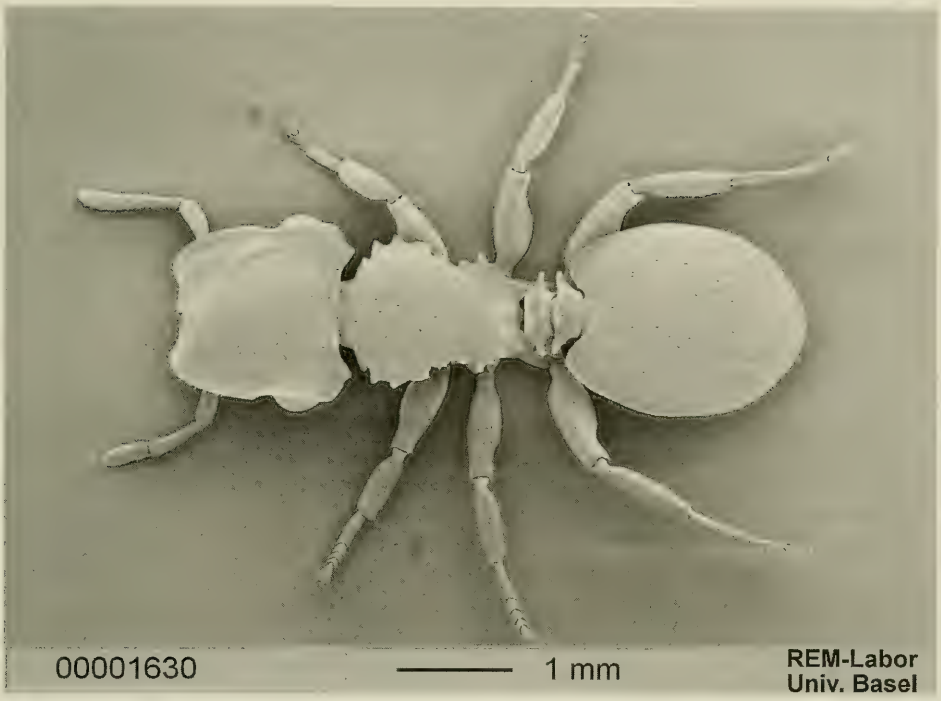


Fig. 330. *Cephalotes angustus* (MAYR). Worker from Botucatu (São Paulo), Brazil in dorsal view.

Zacryptocerus angustus (MAYR), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.
Cephalotes angustus (MAYR), BARONI URBANI, 1998: 320, fig. 2. Worker and soldier, caste polymorphism. First combination in *Cephalotes*.

D i a g n o s i s . - A member of the *angustus* clade differing from its closest outgroup species, *targionii*, in the worker, by the marginate gaster, and, in all female castes, by the anterior face of the petiole less oblique and more truncate and, from the ingroup species, *pallidicephalus*, in the worker, soldier and gyne by the absence of longitudinal rugosities on the first gastral sternite.

W o r k e r (Figs. 330, 375) (description of KEMPF, 1958 a). - "Total length 4.0–6.2 mm; maximum length of head 1.18–1.75 mm; maximum length of thorax 1.18–1.82 mm. Black; the following ferruginous: apex of mandibles, scape and last funicular segment, edge of frontal carinae and occipital lobes, tibiae, the four apical tarsites, anterolateral corners of gaster just inside of the pale, translucid crest; remaining portions of frontal carinae pale testaceous.

Head subopaque, subquadrate; its maximum length subequal to the distance between the eyes, usually slightly longer. Clypeal suture vestigial. Lateral border of head slightly diverging caudad, the posterior portions distinctly sinuate and upturned above eyes. Occipital corners obliquely truncate, the inner angle of the truncation forming a toothlike, apically rounded, projecting lobe. Occipital border deeply emarginate. Dorsal face of head moderately convex discally, finely reticulate-punctate, more sparsely covered with squamiferous foveolae, which become more numerous and crowded toward the occipital border. Lower face of head finely reticulate-punctate, somewhat shiny, and reticulate-rugose discally and cephalad.

Thorax subopaque. Anterior border of pronotum oblique laterad, straight and transverse mesally. Shoulders subacute. Sides of pronotum with two approximated triangular teeth,

followed by a more or less sinuate, or even very obtusely angulate, crest, the posterior corner rectangular or obtuse. Promesonotal suture vestigial or absent. Mesonotum with a blunt or rectangular tooth projecting from each side. Mesoepinotal suture vestigial or absent, usually marked only near the lateral border. Lateral border of basal face of epinotum tridentate: the first tooth, forming the anterior corner of the basal face, small and subrectangular, followed by a second, much larger, acute tooth, and a third, again smaller, tooth, which however is acute and usually points more or less caudad. Between the second and third tooth often a minute, scarcely visible, denticle. Declivous face discally excavated, relatively well differentiated from the basal face, its lateral borders marginate. Dorsum of thorax finely reticulate-punctate rather densely covered with squamiferous foveolae, especially so along the lateral border. Laterotergite of pronotum with a few longitudinal rugosities near its inferior border. Thoracic pleura densely covered with squamiferous foveolae. Fore coxae reticulate-punctate.

Peduncular segments subopaque, the dorsolateral sculpture as on dorsum of thorax and head. Petiole subequal in width to postpetiole, its anterior face obliquely truncate, finely reticulate-punctate and somewhat shining, its superior corners slightly projecting above the dorsal face in the form of a pair of very small denticles. Anterior corners of petiole rounded, the sides with an acute spine, pointing laterad and slightly caudad. Postpetiole with a similar, slightly recurved spine on each side, its dorsal face strongly convex, both longitudinally and transversely.

Gaster subopaque, elliptical, strongly emarginate antero-mesially, the anterolateral border with a hyaline, thin crest, which extends backwards on the sides beyond the conspicuous stigma of the first tergite, and continues caudad as a distinct margination reaching almost the posterior border of the same tergite, which is finely reticulate and superficially foveolate. Foveolae longer and smaller than on thorax. First sternite finely, yet sharply reticulate-punctate, usually without longitudinal rugosities.

Standing hair on mandibles, anterior border of clypeus, along the edge of the frontal carinae and the posterior border of the gastral tergites and sternites. Decumbent hair in the form of short, thick, canaliculate, highly shining scales, on the dorsum of body, cheeks, pleura, and extensor face of femora. Similar scales, but longer, simple on the sides of femora, tibiae, lower face of head and the first gastral sternite."

Measurements (in mm) and indices: TL 4.40–6.58; HL 1.08–1.48; HW 1.26–1.74; EL 0.29–0.40; PW 1.00–1.52; PeW 0.62–0.78; PpW 0.62–0.81; HBaL 0.44–0.64; HBaW 0.10–0.16; CI 112.3–120.0; PI 117.1–131.20; PPeI 161.3–194.9; PPpI 161.3–193.9; HBaI 22.7–26.7.

S o l d i e r (Fig. 374) (description of KEMPF, 1958 a). - "Total length 6.2–8.5 mm; maximum length of head 1.85–2.50 mm; maximum length of thorax 1.78–2.28 mm. Black; upper half of sides of head and floor of cephalic disc more or less reddish-brown, the latter usually, not always, with a large, elongate, anteromedian black spot; marginate edge of cephalic disc infuscated; tip of scape, tibiae, tarsites ferruginous; extensor face of tibiae lighter in color; first gastral tergite with the customary four yellowish spots, the pair of each side often confluent.

Head somewhat shiny; surmounted by a subquadrate, very seldom elongate, flat, completely marginate disc. Borders of disc scarcely crenulate and very little raised, not concealing the floor of the cephalic disc, when seen in profile. Anterior portion of disc semicircular, its sides subparallel up to some distance behind the posterior border of the eyes, where they form an obtuse angle and converge strongly mesad to meet the truncate, straight, transverse posterior border. Clypeal sutures vestigial. Floor of disc slightly excavate and a little transparent above the antennal scrobes. Occipital lobes sharply marginate, their lateral border convex, forming a blunt tooth at the posterior corner. Floor of disc and sides of head very finely and densely punctate, more sparsely foveolate. Lower face of head more shiny, microsculpture and foveolae more superficial, the latter very sparse.

Thorax shiny on dorsum, opaque on sides. Pronotum nearly as broad as head, its anterior angle with a triangular tooth, its sides excised behind the tooth, then convex at the level of the transverse carina, the following part strongly converging mesad and a little sinuous. Transverse pronotal carina usually very pronounced, the lateral portions concave, strongly raised and sharply edged, the median portion convex, less prominent, only bluntly marginate in the

middle. Promesonotal suture usually only vestigial. Sides of mesonotum with an obliquely truncate, projecting, marginate lateral lobe. Mesoepinotal suture deeply impressed laterad, slightly marked or only vestigial or even absent in the middle. Basal face of epinotum very short and broad, its sides with a broad triangular tooth and its posterior corner with a strong tooth projecting upward and laterad. Sculpture of dorsum of thorax as on floor of cephalic disc, the squamiferous foveolae smaller and more crowded. Laterotergite of pronotum very sparsely foveolate, usually with a few rugosities near the inferior border. Pleura more densely foveolate on the inferior half. Fore coxae occasionally with a few transverse rugosities on the external face, near the apex, but usually only reticulate-punctate. Peduncular segments, in general, as in worker, the lateral spines stouter, solid, those of petiole more conspicuously recurved.

Gaster elliptical, the tergites subopaque, the sternites slightly more shining. Distinctly emarginate anteromesially at the postpetiolar insertion, the anterolateral border sharply marginate, the anteriormost portion usually very narrowly crested. Lateral margination of first tergite ending near the stigma. First tergite finely reticulate-punctate, the squamiferous foveolae more superficial and elongate. First sternite similarly sculptured, often with a few fine longitudinal rugosities anterolaterally.

Standing hair on mandibles and tip of gaster. A fringe of very sparse and thickish hair projecting from the anterolateral border of the cephalic disc. Squamiform hair decumbent, always in foveolae, similar to those of worker, always highly shiny, with reflexes of polished brass."

Measurements (in mm) and indices: TL 6.96–8.92; HL 1.64–2.46; HW 1.84–2.60; EL 0.39–0.48; PW 1.64–2.60; PeW 0.72–0.95; PpW 0.72–1.00; HBaL 0.58–0.73; HBaW 0.16–0.22; CI 105.7–112.2; PI 100.0–112.2; PPeI 226.4–273.7; PPpI 221.5–260.0; HBaI 27.6–30.1.

G y n e (Figs. 331, 373). - Head with a complete disc, weakly concave anteriorly and gently convex posteriorly. Frontal carinae superficially crenulate. Sides of the disc converging before the eyes and connected posteriorly by a truncate or convex border. Vertexal angles convex and with a well marked obtuse margin. Clypeal border concave and with a pair of external denticles. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a thick carina ending in a small denticle just before the eyes. Eyes gently convex and not hidden by the disc.

Mesosoma. Anterior pronotal border convex and covering the scapular angles in dorsal view in most specimens. Pronotal carina visible but superficial on the sides. Mesonotum and scutellum on the same plane and flat. Propodeum well differentiate in basal and declivous faces. Basal face with subparallel sides, slightly converging posteriorly and bearing a pair of small denticles and a pair of triangular teeth slightly diverging. Sides of the declivous face converging posteriorly.

Anterior face of the petiole oblique. Sides of the petiole with a small denticle. Postpetiole convex and with an incomplete V-shaped carina in the middle. Postpetiolar sides with a pair of thick, pointed spines arising from the anterior border and directed anterolaterally.

Gaster oval, with a pair of broad, protruding anterolateral lobes. Anterolateral borders of the first gastral tergite with a very narrow margin not reaching the stigma posteriorly.

Hind femora without angles or denticles. Hind basitarsi slightly more compressed apically than distally, and with subparallel sides.

Sculpture. Head dorsum minutely and superficially punctate, shining and covered with variably clumped foveae, larger on the frons. Ventral part of the head reticulate-punctate, variably shining and with sparse foveae. Mesonotum, pedicel and distal part of the outer face of the femora and outer face of the tibiae reticulate-punctate, with foveae of different size and variably clumped, more round on the pronotum, mesonotum and scutellum, denser on the basal face of the propodeum, on the pedicel and on the upper mesopleurae. Gaster and remaining parts of the legs reticulate-punctate. Anterior fifth of the first gastral tergite with superficial foveae. Some specimens with the sides of the first gastral sternite with few, irregular, longitudinal rugosities.

Wings as in Fig. 331.

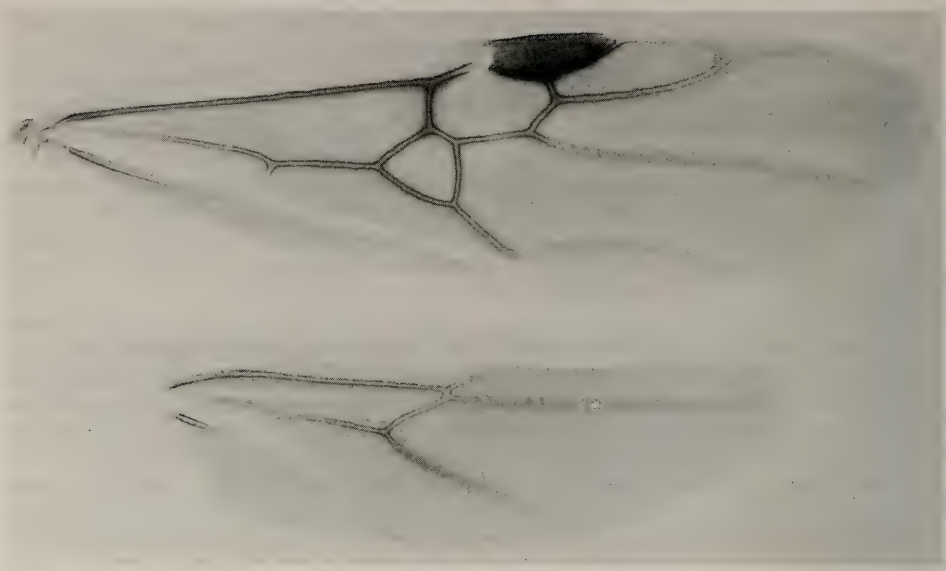


Fig. 331. *Cephalotes angustus* (MAYR). Gyne from Botucatu (São Paulo), Brazil, fore and hind wings.

Pilosity. Each fovea with an appressed canaliculate hair. Body parts without foveae with sparse, appressed, thin, slightly canaliculate hairs. Sides of the frontal carinae and of the disc, mesonotum, pedicel, gaster and legs with sparse, slightly clubbed, erect hairs. First gastral sternite with rare, long, subtruncate, erect hairs.

Colour. Black. Upper half of the head dorsum dark orange to light brown with blackish frons. First gastral tergite with two pairs of orange-reddish spots, the first pair anterolateral and the second one close to the posterior border; few specimens without or with spots poorly developed; sometimes the first gastral tergite with a long, yellow strip on the sides. Femora dark brown to black, sometimes the distal half of the fore femora dark orange-brown. Tibiae and tarsomeres dark orange to brown, tarsi darker.

Measurements (in mm) and indices: TL 9.12–11.38; HL 1.92–2.40; HW 1.88–2.52; EL 0.41–0.50; PW 1.76–2.40; PeW 0.72–0.90; PpW 0.81–1.08; HBaL 0.64–0.80; HBaW 0.18–0.27; CI 97.9–105.0; PI 100.0–108.5; PPeI 231.6–266.7; PPpI 207.4–222.2; HBaI 27.5–32.5.

M a l e (Fig. 332). - Differing from that of *targionii* in the following details:

Head more convex dorsally. Vertexal angles obtuse. Frons flat. Mesosoma more robust. Anterior pronotal border straight. Humeral angles weakly marked. Pronotal sides subparallel. Petiole and postpetiole shorter and broader. Sides of the postpetiole with a larger denticle. Gaster narrower than the mesosoma.

Sculpture. Body less shining, more opaque and covered by more impressed reticulation. Head, mesosoma and sides of the pedicel with superficial foveae; the foveae separate by irregular, short rugosities on the head, denser on the posterior third of the head dorsum, on the pronotum and on the basal face of the propodeum. Basal face of the propodeum with additional, irregular rugosities between the foveae. Pleurae with few longitudinal rugosities. Pedicel with few, thin, longitudinal rugosities. Gaster and legs reticulate, the reticulation more impressed on the first tergite.

Genitalia as in Fig. 333.

Wings as in the gyne.

Pilosity. Erect hairs shorter and sparser, less abundant on the posterior borders of the gaster.

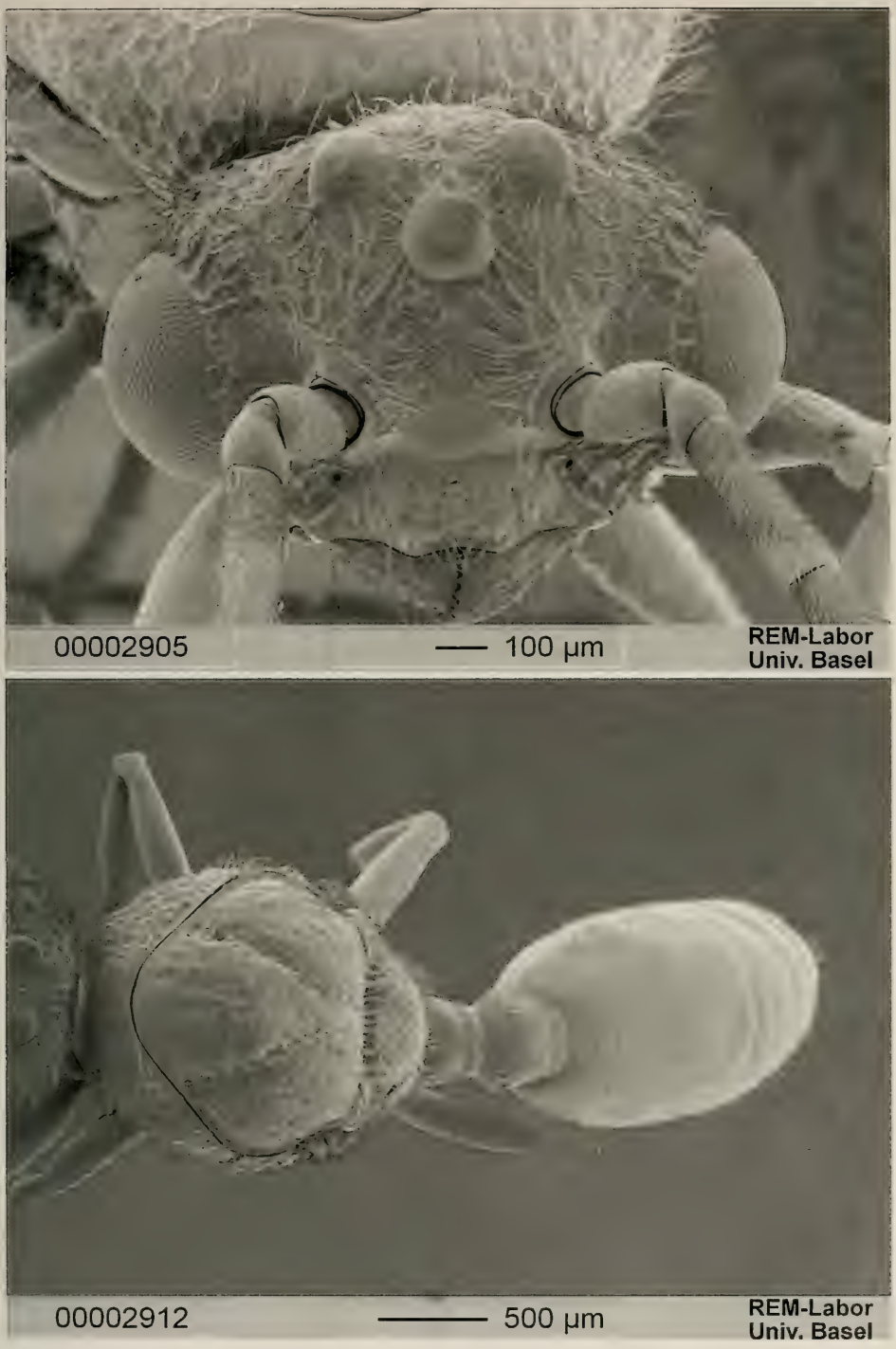


Fig. 332. *Cephalotes angustus* (MAYR). Male from Botucatu (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Colour. Head, mesosoma, pedicel, gaster and coxae black. Proximal half of the femora light brown. Remaining parts of the legs yellowish.

Measurements (in mm) and indices: TL 5.18–6.40; HL 0.80–0.96; HW 1.00–1.22; EL 0.43–0.55; PW 1.04–1.28; PeW 0.43–0.55; PpW 0.46–0.60; HBaL 0.55–0.75; HBaW 0.07–0.12; CI 125.0–127.1; PI 95.3–96.1; PPeI 232.7–241.9; PPpI 213.3–226.1; HBaI 12.7–14.7.

Material examined. - **Brazil**: no further locality, 1 soldier (holotype of *cristatus* var. *ruficeps*), K. ZUBACK [NHMB]; no further locality, 2 workers, 1 soldier, 1 male [MCSN]; 2 workers, 1 soldier (labelled as syntypes of *angustus*) [MHNG]. Bahia: no further locality, 1 gyne, R. OBERTHUR, 1913 [MNHN]; Ilhéus, 20.IV.1993, 1 worker, EDUARDO [MZSP]. Minas Gerais: Serra da Caraça, 1380 m, X.1961, 2 workers, KLOSS et al. [MZSP]; Manhumirim, 17.IV.1962, 9 workers, 5 soldiers, 1 gyne, F. M. OLIVEIRA [MZSP]; Pedra Azul, 800 m, XI.1972, 3 workers, SEABRA & ALVARENGA [MZSP]. São Paulo: no further locality, 1 soldier, JHERING [MHNG]; Anhembi, Fazenda B. Rico, 14.II.1969, 1 worker, MAGALHÃES et al. [MZSP]; Agudos, Set. 1954, 2 workers, R. MUELLER [MCZC]; same locality, 3.X.1954, 7 workers, 5 soldiers, W. W. KEMPF [MCZC, MZSP]; same locality, 10.I, 20.XI.1955, 2 workers, W. W. KEMPF [MCZC, MZSP]; São Paulo, 1 worker, F. LANE [MZSP]; São Paulo, Santo Amaro, 15.X.1928, 1 worker, MELZER [MZSP]; Boracéia, 05.II.1960, 1 worker, F. LANE [MZSP]; Raiz da Serra, 1 soldier, 1 male [MZSP]; same locality, 10.XII.1906, 1 worker, 1 soldier, H. LUEDERWALDT [MZSP]; Caraguatatuba, Res. Flor., 680 m, 02.IV.1962, 1 worker, 2 soldiers, K. LENKO [MZSP]; Juquiá, Fazenda Lagoinha, 17.VI.1964, 55 workers, 4 soldiers, F. LANE [MZSP]; Peruibe, 05.IX.1988, 1 worker, M. L. DE ANDRADE [NHMB]; Botucatu, 28.I.1996, workers, soldiers, gynes and males, M. L. DE ANDRADE [CPCC, LACM, MCZC, MNHN, ZSMC, USNM]. Rio de Janeiro: no further locality, 1 gyne, GÖLDI [MHNG]; no further locality, 9 workers (syntypes of var. *clarior*), GÖLDI [MHNG, NHMB]; Corcovado, 07.IX.1891, 2 workers [ZSMC]; same locality, 10 & 12.XI.1958, 2 gynes, 1 male, SEABRA & ALVARENGA [MZSP]; Nova Friburgo, April - May 1884, 1 worker, P. GERMAIN [MCSN]; same locality, 1 worker, GÖLDI [MHNG]; Rio de Janeiro, Oct., Nov. Dec., Jan. 1937–38, 1 gyne, R. C. SHANNON [USNM]; Represa Rio Grande, Guanabara, 2–6.IX, 13–15.X, 14–17.XI.1960, 15.III.1961, 1 worker, 3 soldiers, 2 gynes, F. M. OLIVEIRA [MZSP]; Terezópolis, 2–5.XII.1958, 1 worker, MARTINEZ et al. [MZSP]. Paraná: Rio Negro, V.1959, 4 workers, 1 soldier, L. SCHMITT [MCZC]; same locality, XII.1955, 3 workers, R. MÜLLER [MZSP]; Arapongas, Col. Esperança, 26.VII.1955, 8 workers, W. W. KEMPF [MCZC, MZSP]; same locality, 2 workers, REICHENSPERGER [NHMB]; Rolândia, 05.XI.1951, 05.IV.1953, 15.IV.1954, IX.1959, 15.XI.1961, 11 workers, W. W. KEMPF [MZSP]. Santa Catarina: no further locality, 17 workers, 3 gynes, SCHMALZ [MCSN, MHNG, USNM]; Itajaí, 1928, 33 workers, 10 soldiers, 7 males, FONTES [MCZC, MZSP]; Gaspar, 1928, 1 worker, M. SILVA FONTES [MZSP]; Gaspar, Poço Grande, XII.1953, I.1958, 2 workers, R. MÜLLER [MZSP]; Blumenau, 1 worker, REICHENSPERGER [NHMB]; Nova Teutônia, II.1960, X.1962, VI.1963, X.1965, X.1973, XII.1974, X.1975, 13 workers, 9 soldiers, Fritz PLAUMANN [MZSP]; S. Teresa, 10.IV.1952, 1 worker, BILBERT [MZSP]. Rio Grande do Sul: no further locality, 2 workers, JHERING [MCSN]; Pareci Novo, 18.XI.1925, 1 worker, 1 soldier, B. RAMBO [MZSP].

Discussion. - *C. angustus* is the largest species of the *angustus* clade; except for the size, which is often subject to individual variation, it is very similar to *targionii*, *notatus* and *pallidicephalus*.

Angustus exhibits great variability, the most important traits of which appear to be: in the workers, the sides of the pronotum may have three or four denticles and those of the propodeum three to five (those with 4–5 denticles correspond to FOREL's var. *clarior*); the maculae of first gastral tergite vary in width and length; the frontal carinae may be more or less upturned over the eyes; the vertexal angles bear lamellae developed to different extents; the first gastral sternite may bear on the sides only few, irregular, longitudinal, thin, rugosities; in the soldiers and in the gynes, the floor of the disc can be flat or slightly convex, the foveae on the disc more or less

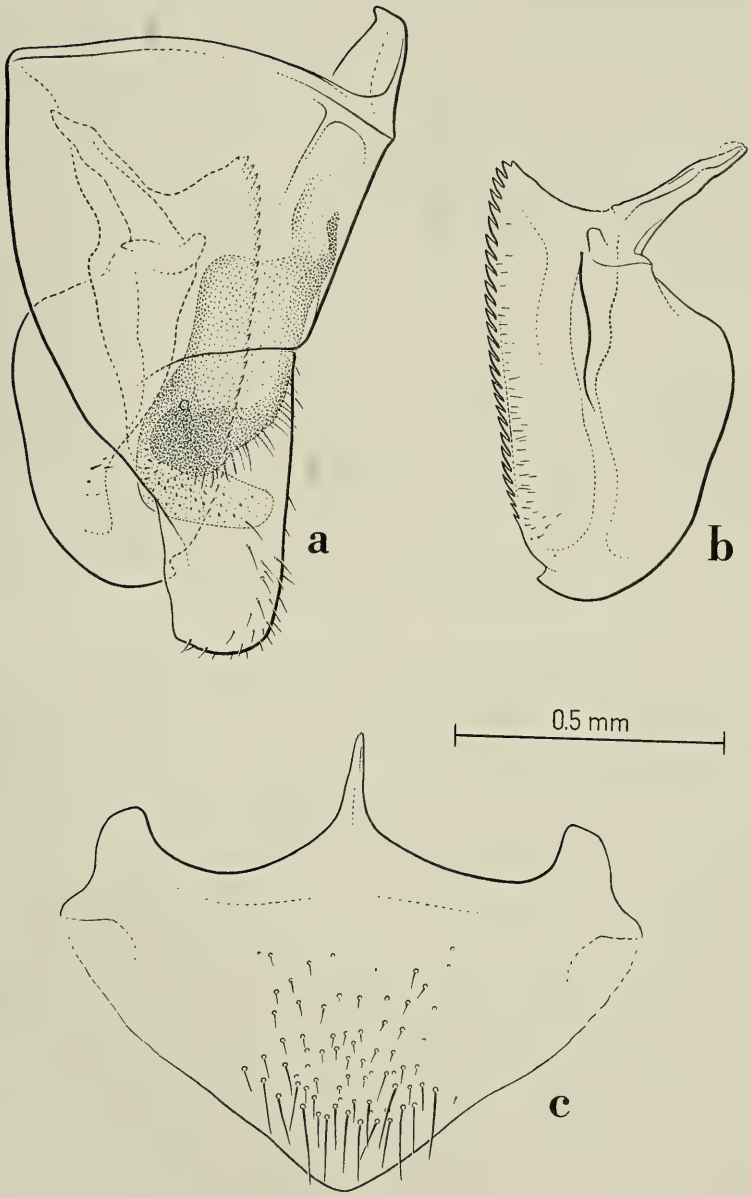


Fig. 333. *Cephalotes angustus* (Mayr). Male from Botucatu (São Paulo), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

dense, the frons may bear or not a black spot, the pronotum may have a lateral pair of yellow to dark red strips of variable size, the gastral spots may vary in colour and size or may be fused in a long yellow strip. The density of the disc foveae is particularly great in the unique type of the var. *ruficeps* SANTSCHI (Brazil) and among three soldiers and two gynes from Represa Rio Grande, Guanabara (Rio de Janeiro): they might represent a separate species. On the other hand, we have seen specimens of undoubted *angustus* from other localities of the same state.

This species is reported from Argentina by KEMPF (1958 a). We did not see Argentinean material of *angustus* but we have no reasons to doubt this record.

D i s t r i b u t i o n : Brazil and Argentina.

Cephalotes pallidicephalus (SMITH) bona species, new combination
Figs. 334, 335, 336, 337, 338

Cryptocerus pallidicephalus SMITH, 1876: 606, pl. 11 fig. 5. Gyne. Original description. Type locality: Mexico (probably erroneous). Type material: holotype gyne labelled "*Cryptocerus pallidicephalus*, (type) Smith, Mexico" in BMNH (KEMPF, 1964 a: 438), examined.

Cryptocerus striativentris EMERY, 1894 a: 203, figs. 10–12. Worker, soldier. Original description. Type locality: Santa Catarina. Type material: 1 worker labelled "Santa Catarina, Mayr", MCSN; 2 workers, 1 soldier labelled "Itajahy, Bresil, F. Müller", MCSN; also probably belonging to the type series: 9 workers, 4 soldiers (some pins with cotype label) in MHNG; 1 worker, in NHMB; 1 soldier, in MCZC; all examined. N e w s y n o n y m.

Paracryptocerus striativentris (EMERY), KEMPF, 1958 a: 80, pl. 1, fig. 1, 6, pl. 3, fig. 3, pl. 5, fig. 3, pl. 6, fig. 4. Worker, soldier and gyne. First combination in *Paracryptocerus*.

Paracryptocerus scutulatus (SMITH), KEMPF, 1964 a: 438. Nec SMITH, 1867. Misidentification.

Zacryptocerus striativentris (EMERY), BRANDÃO, 1991: 388. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *angustus* clade differing from all the other species of the genus by the first gastral sternite of the worker covered with thick, longitudinal striation. In addition, it differs from the two species of its sister clade (*notatus* and *goeldii*) in the soldier and gyne by the border of the disc less raised, and by the vertexal angles and the pronotal sides with a narrower lamellaceous border.

W o r k e r (Fig. 334) (description of KEMPF, 1958 a sub *striativentris*). - "Total length 3.1–4.8 mm; maximum length of head 0.89–1.35 mm; maximum length of thorax 0.89–1.35 mm. Black; the following ferruginous: tip of mandibles, funicular segments II - IV, antero-lateral corners of gaster, just inside of the pale, translucid crest; light brown: edge of frontal carinae, tip of scape, funicular segment I, tip of femora, tibiae, tarsites; pale-testaceous: remaining portion of frontal carinae.

Head subopaque, subquadrate; slightly more elongate than in *angustus*, the maximum length always somewhat exceeding the interocular width. Clypeal suture vestigial. Lateral border of head somewhat diverging caudad, distinctly emarginate in front of, convex and slightly upturned above, eyes. Occipital corners obliquely truncate, the truncated edge either notched or straight, the inner angle never forming a prominent triangular tooth. Occipital border gently concave. Dorsal face of head gently convex, finely reticulate-punctate, more sparsely covered with squamiferous foveolae, which increase in number toward the occipital border. Lower face of head finely reticulate-punctate, sparsely and very superficially foveolate, the foveolae very elongate.

Thorax subopaque. Anterior border of pronotum very gently convex, almost straight. Shoulders rectangular. Lateral border of pronotum quite variable, even in specimens of the

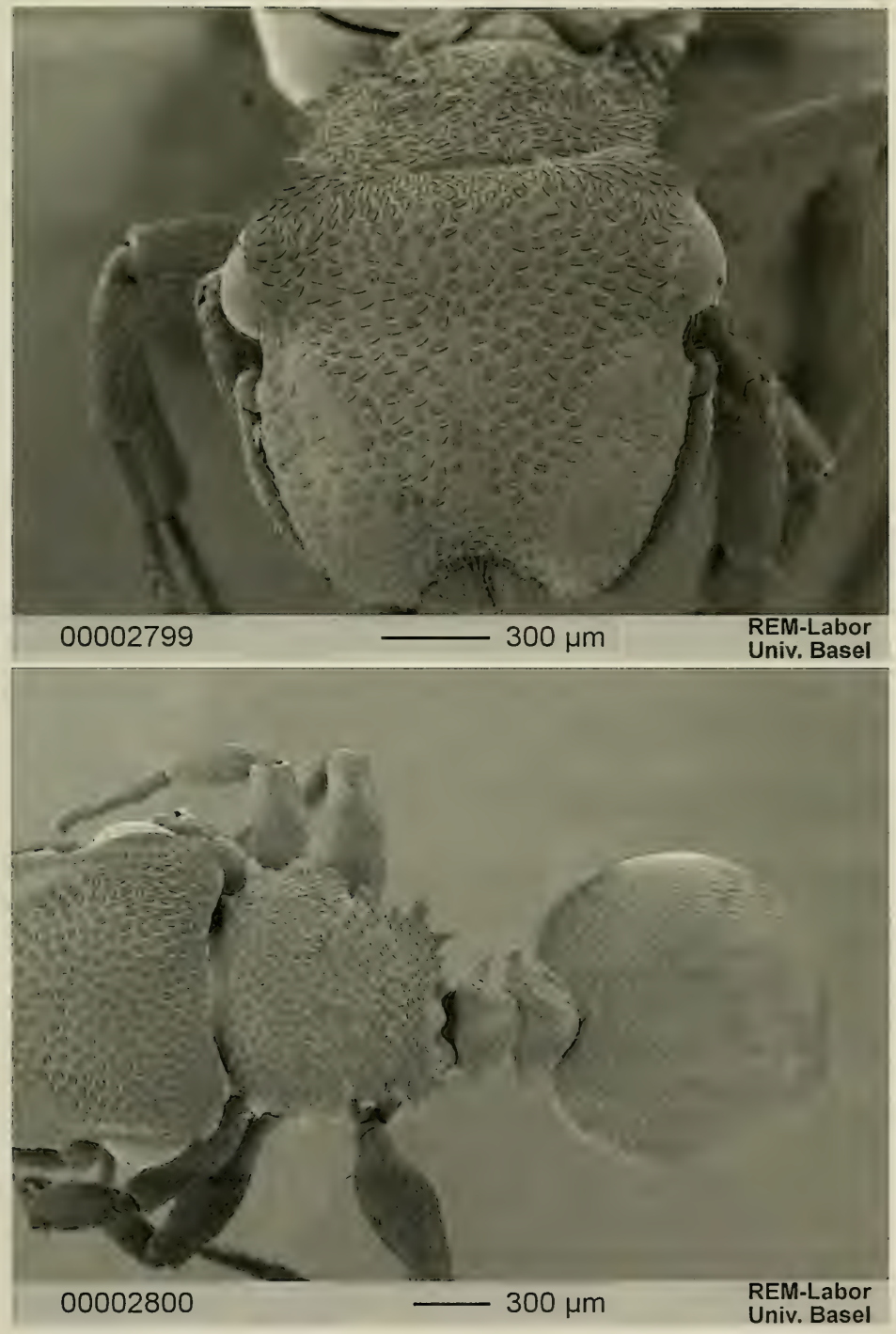


Fig. 334. *Cephalotes pallidicephalus* (SMITH). Worker from Ilha da Vitoria (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

same nest. Typically there is a triangular or subacute tooth next to the scapular corner, followed by a sharply marginate, often irregularly crenate or denticulate crest. Especially in very small specimens, this crest presents occasionally two distinct, though apically rounded or truncate, rather foliaceous teeth, so that in this case the sides of the pronotum are really tridentate. Posterior corner of pronotum subrectangular. Promesonotal suture vestigial or absent. Mesonotum with a laterally projecting tooth on each side, which is subacute in small specimens, blunt, broadly and obliquely truncate in larger specimens. Occasionally there is a minute and sharp tooth behind the preceding tooth. Mesoepinotal suture usually absent, seldom vestigial. Lateral border of basal face of epinotum tridentate, all three teeth usually acute, the second by far the largest. Behind the third tooth, on the marginate border of the declivous face one or two very small denticles may be present. Declivous face continuous with basal face, not clearly separable from each other, forming in profile a gentle and even curvature. Dorsum of thorax finely reticulate-punctate and foveolate, in the same fashion as dorsum of head, but the foveolae are more numerous and crowded, so that on the mesoepinotum the integument becomes reticulate-rugose. Laterotergite of pronotum with longitudinal striae. Thoracic pleura principally longitudinally rugose with very densely interspersed squamiferous foveolae. Fore coxae coarsely and obliquely striate on the outer face.

Peduncular segments subopaque, the dorsolateral sculpture as on head and thorax. Petiole subequal in width to the postpetiole, its anterior face obliquely truncate, finely reticulate-punctate, usually not sharply marginate nor denticulate at its point of contact with the dorsal face, but sometimes as in *angustus*. Lateral spines of both segments depressed, platelike, foliaceous, semitransparent, more recurved than in *angustus*. Dorsal face of postpetiole more gently convex than in *angustus*.

Gaster subopaque, elliptical, strongly emarginate antero-mesially, the anterolateral border with a transparent thin crest, which extends backwards beyond the conspicuous stigma of the first gastral tergite, which is very sharply reticulate-punctate, and covered with superficially impressed elongated squamiferous foveolae. First sternite, as a rule, very coarsely and regularly longitudinally striate.

Pilosity essentially the same as in *angustus*."

Measurements (in mm) and indices: TL 3.80–5.16; HL 0.98–1.30; HW 1.04–1.44; EL 0.28–0.34; PW 0.92–1.26; PeW 0.50–0.66; PpW 0.54–0.71; HBaL 0.35–0.43; HBaW 0.07–0.11; CI 106.0–110.8; PI 112.8–117.4; PPeI 173.3–190.9; PPpI 164.9–177.5; HBaI 20.5–25.6.

S o l d i e r (Fig. 335) (description of KEMPF, 1958 a sub *striativentris*). - "Total length 4.7–6.3 mm; maximum length of head 1.46–2.00 mm; maximum length of thorax 1.32–1.64 mm: Black; the following yellowish-brown: lateral portions of transverse carina, edge of lateral lobes of mesonotum, teeth of basal face of epinotum, apical half of extensor face of femora; ferruginous: mandibles, edges of yellowish-brown markings on thorax and gaster, tarsites; testaceous: tibiae, the four spots on the first gastral tergite, which in full grown workers are fused in a horseshoe-like fashion, as shown by the figure. All sharply marginate edges inside the light areas are conspicuously darker.

Head subopaque, surmounted by an oval, somewhat excavated, disc. Borders of disc scarcely crenulate, conspicuously raised and upturned laterally, concealing the floor of the disc, when seen in profile. Occipital border of disc not raised, round, not truncate. Clypeal suture, at most vestigial, usually absent. Floor of disc, except for the raised lateral borders, rather flat, with a very gentle anteromedian convexity, flanked by very shallow concavities above the antennal scrobe, where the integument is somewhat transparent. Occipital lobes sharply marginate, the lateral border gently convex, the posterior angle obtuse. Floor of disc and sides of head finely reticulate-punctate, coarsely reticulate-rugose and foveolate, the squamiferous foveolae much broader than the raised intervals. Lower face of head rather shiny, almost smooth postero-laterally, with very superficial microsculpture and sparse foveolae.

Thorax subopaque dorsally, opaque laterally. Pronotum nearly as broad as head, its anterior corner with a triangular tooth, its sides slightly excised behind the tooth, then convex at the level of the transverse carina, then strongly converging mesad toward the mesonotum.

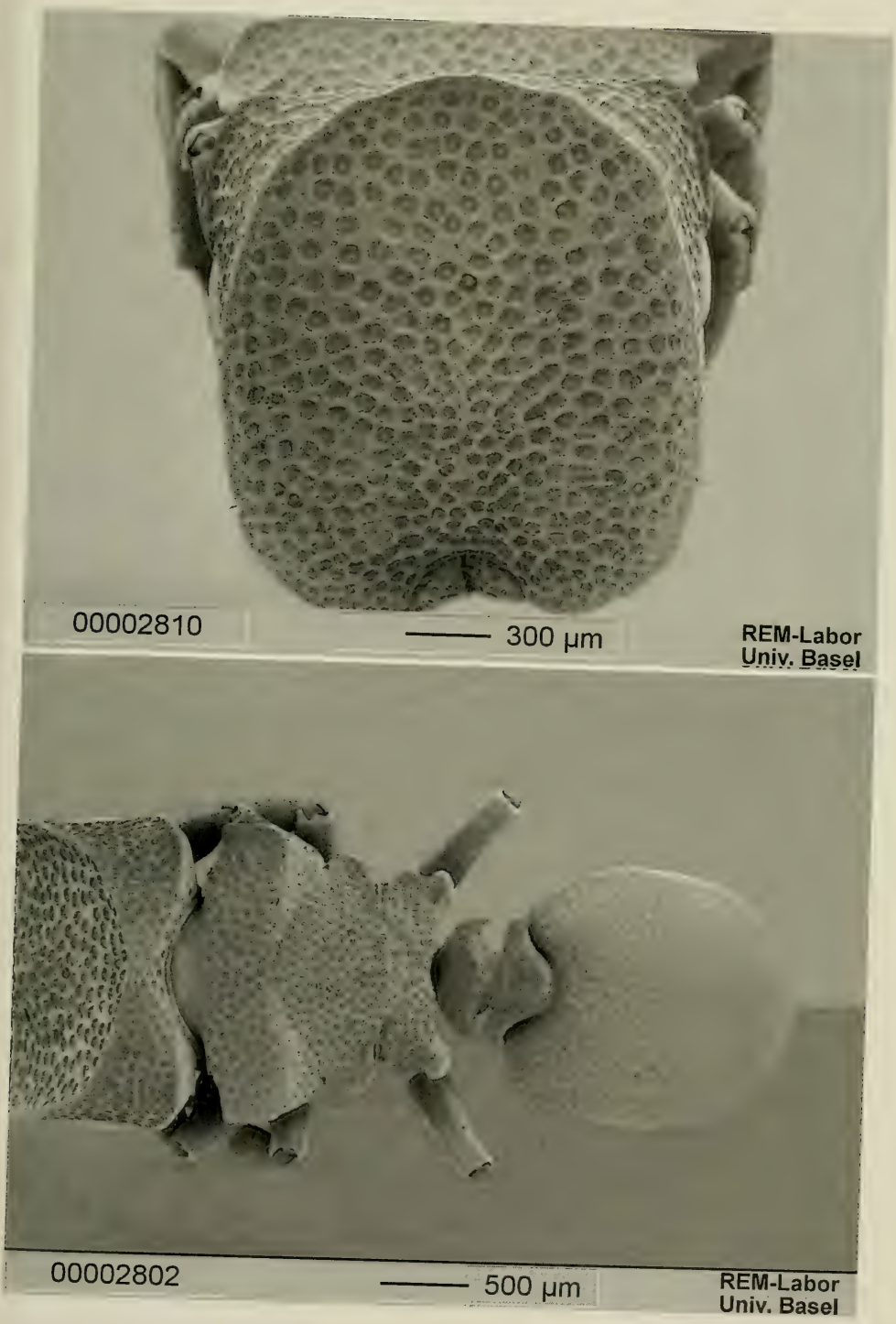


Fig. 335. *Cephalotes pallidicephalus* (SMITH). Soldier from Ilha da Vitoria (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Transverse pronotal carina, as seen from the front, very deeply excised in the middle, concave laterally, when seen from above; very prominent and sharply edged, excepting the mesial notch. Promesonotal suture vestigial. Mesonotum with a broad, obliquely truncate and marginate projecting lobe on each side. Mesoepinotal suture deeply impressed laterally, usually well marked but superficial mesially. Basal face of epinotum very short and broad, its lateral border with a triangular tooth and its posterior corner with a very stout, apically rounded tooth which points upward and laterad. Dorsum of thorax finely reticulate-punctate, sparsely foveolate on pronotum, more densely foveolate on mesoepinotum, the foveolae much smaller than those on cephalic disc. Laterotergite of pronotum sparsely foveolate and somewhat rugose. Pleura mainly foveolate. Fore coxae slightly rugose on the outer face.

Peduncular segments as in worker, but the petiole is distinctly narrower, bearing on each side a short tooth, which points obliquely caudad. Postpetiole, as seen in profile, conspicuously convex above, its lateral spines solid, not platelike.

Gaster subopaque, the thin anterolateral crest and the lateral margination of the first gastral tergite as in *angustus*, the sides of gaster, however, less convex. First gastral sternite longitudinally striato-rugose, striae not as coarse as in worker.

Pilosity as in *angustus*, except for the hair arising from the pits of the cephalic disc, which is minute, scarcely visible, not glittering, nor strictly decumbent."

Measurements (in mm) and indices: TL 5.32–6.50; HL 1.52–1.80; HW 1.52–1.76; EL 0.36–0.41; PW 1.44–1.68; PeW 0.56–0.65; PpW 0.65–0.72; HBaL 0.39–0.42; HBaW 0.10–0.11; CI 97.8–100.0; PI 104.8–106.4; PPeI 240.0–278.6; PPpI 221.5–233.3; HBaI 25.6–26.2.

G y n e (Fig. 336) (description largely based on the holotype and completed after examination of additional specimens). - Head disc present. Head dorsum slightly concave on its anterior half and flat posteriorly. Frontal carinae expanded anteriorly, converging posteriorly and connected with the convex posterior border of the disc. Vertexal angles convex and with strongly marginate border. Eyes weakly convex and visible in full face view. Ocelli far from the posterior border of the head disc. Dorsal border of the antennal scrobes with a thick carina ending in a small, obtuse denticle just before the eyes. Anterior clypeal border concave. Mandibles with a lateral carina and partially hidden by the frontal carinae.

Mesosoma. Humeral angles obtuse and marginate. Pronotal sides straight. Pronotal carina marked, shortly interrupted in the middle. Promesonotal suture impressed. Lower mesopleurae with a denticle. Mesonotum and scutellum almost flat. Propodeum differentiated in basal and declivous face; basal face short, little convex dorsally and with a superficial furrow in the middle; its sides with two pairs of short, triangular teeth, the anterior pair on the beginning of the basal face, separate from the second pair by the converging sides; declivous face concave in the middle.

Petiole with distinctly differentiated anterior and posterior faces; anterior face oblique; posterior face flat; sides of the petiole with a pair of small denticles pointed backwards. Postpetiole broadly convex; postpetiolar spines arising from the anterior border of the petiole and recurved.

Gaster with an anterolateral lamella, not reaching the stigma.

Legs. Fore coxae with a round denticle anteriorly. Mid and hind femora without angles or denticles. Mid and hind basitarsi with subparallel sides and slightly narrow at base.

Sculpture. Head dorsum with deep, anastomosing foveae. Sides of the head with the same type of sculpture as the head dorsum but smaller and shallower. Ventral part of the head superficially and minutely punctate, slightly shining and with rare, superficial foveae. Mesosoma and pedicel superficially reticulate-punctate and covered by smaller foveae than those on the head dorsum, broader than their interspaces, denser on the mesopleurae, on the scutellum, on the basal face of the propodeum, on the sides and on the posterior face of the petiole and on the postpetiole. Propleurae and metapleurae reticulate-punctate and rarely foveolate. Declivous face of the propodeum, anterior face of the petiole, legs and gaster reticulate-punctate. Very superficial, sparse, small, piligerous foveae on the anterior third of

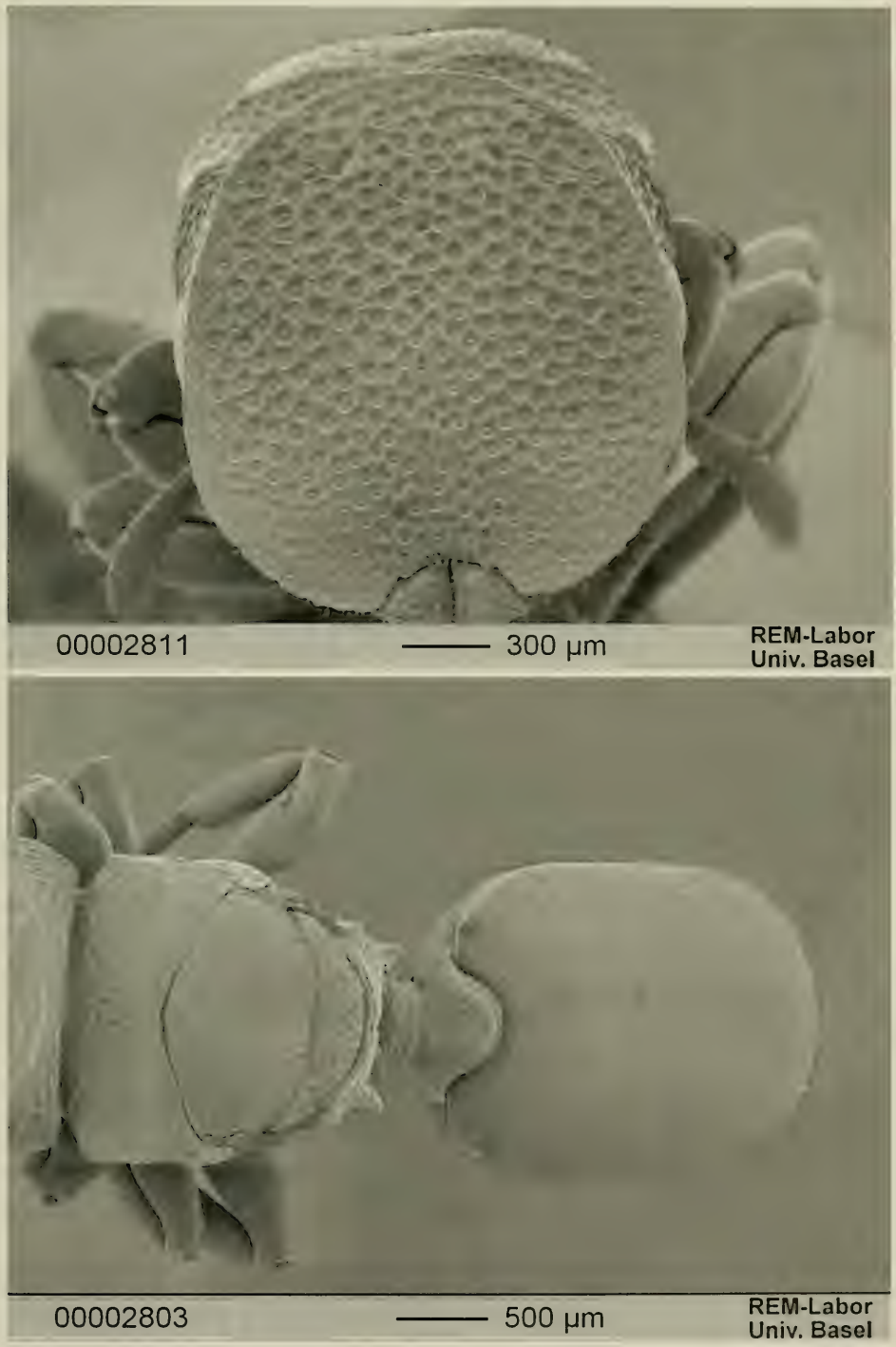


Fig. 336. *Cephalotes pallidicephalus* (SMITH). Gyne from Ilha da Vitoria (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

the gaster; similar foveae on the outer face of the tibiae. Sides of the first gastral sternite with longitudinal rugae.

Pilosity. Most of the foveae with a slightly canaliculate hair, suberect on the head dorsum and appressed on the other foveae. Borders of the disc and few foveae on the mesosoma and on the pedicel with an erect, subclavate hair; similar subclavate hairs on the gaster and on the legs, denser on the posterior borders of the tergites and sternites. Gaster and legs with a additional type of hair: (1) short, appressed and thin.

Colour. Ventral part of the head, clypeus, mesosoma, pedicel, coxae and femora black, gaster lighter. Center of the head disc, humeral angles, tibiofemoral articulations, tarsomeres light brown. Head disc up to the sides and tibiae dark yellow. Gaster with two pairs of broad yellow spots, the anterior pair surpassing the stigma posteriorly and interconnected in the middle, the second pair beginning from the posterior half of the first gastral tergite and almost reaching its posterior border.

Measurements (in mm) and indices: TL 7.40–8.44; HL 1.64–1.80; HW 1.56–1.68; EL 0.38–0.42; PW 1.52–1.60; PeW 0.56–0.64; PpW 0.74–0.80; HBaL 0.48–0.53; HBaW 0.13–0.14; CI 93.3–95.3; PI 102.5–105.0; PPeI 250.0–271.4; PPpI 200.0–213.3; HBaI 25.5–27.1.

Male (Fig. 337) (previously undescribed). - Differing from the male of *angustus* in the following details:

Vertexal angles with a pair of small median denticles. Frontal carinae more marked. Mandibles shorter. Anterior pronotal border straight. Humeral angles well visible, obtuse or weakly pointed. Pronotal sides marginate and parallel. Anterior face of the petiole more concave medially.

Genitalia and subgenital plate as in Fig. 338.

Sculpture. Body less shining, more opaque and covered with deeper reticulation. Head, mesosoma and sides of the pedicel with deeper, irregular foveae separate by irregular, short rugosities on the head, on the pronotum and on the basal face of the propodeum. Pleurae with denser longitudinal rugosities, well impressed on the propleurae, irregular on the metapleurae.

Colour. Head, mesosoma and pedicel black. Coxae and gaster brown, two proximal thirds of the femora lighter. Remaining parts of the legs yellowish.

Measurements (in mm) and indices: TL 5.05–5.44; HL 0.77–0.80; HW 0.94–1.00; EL 0.39–0.40; PW 1.04–1.12; PeW 0.40–0.42; PpW 0.40–0.43; HBaL 0.55–0.58; HBaW 0.06–0.07; CI 122.1–125.0; PI 89.3–90.4; PPeI 260.0–266.7, PPpI 260.0–260.5; HBaI 10.9–12.1.

Material examined. - **Mexico**: no further locality, 1 gyne (holotype) [BMNH]. Surely erroneous locality record.

Brazil: Bahia: Ilhéus, 20.IV.1993, 1 worker, EDUARDO [CPCC]. Minas Gerais: S. Lourenço, Jan. 1957, 1 worker, R. MUELLER [MZSP]. São Paulo: São Roque, 02.I.1972, 1 worker, F. LANE [MZSP]; Barueri, 11.VI.1958, 3 workers, 1 soldier, 1 gyne, K. LENKO [MZSP]; Ilha dos Buzios, 16 & 20.X–04.XI.1963, 59 workers, 15 soldiers, 5 gynes, Exp. Dep. Zool. [MZSP]; same locality, 31.III.1964, 17 workers, 3 soldiers [MZSP]; Ilha da Vitória, 29.III.–06.IV.1965, 41 workers, 13 soldiers, Exp. Dep. Zool. [MZSP]. Rio de Janeiro: no further locality, 3 workers [MCSN]; Campo Belo, 10.XI.1925, 1 gyne, ZIKAN [MCZC]; same locality, 26.X.1925, 3 soldiers, 1 gyne, J. F. ZIKAN [MZSP]; Represa Rio Grande, 15.III.1961, 1 gyne, F. M. OLIVEIRA [MZSP]. Paraná: Rolândia, 05.XI.1951, 30.III.1953, 2 workers, W. W. KEMPF [MZSP]; Motorway BR–2 (São Paulo-Paraná), km 40, V.1960, 1 worker, W. W. KEMPF & SANTOS [MZSP]. Santa Catarina: no further locality, 1 worker [MCSN]; Itajaí, 2 workers, 1 soldier (syntypes of *striativentris*) [MCSN]; same locality, 9 workers, 4 soldiers (probably syntypes of *striativentris*) [MHNG], 1 worker [NHMB], 1 soldier [MCZC]; same locality, 1928, 62 workers, 9 soldiers, 2 gynes, 1 male, M. S. FONTES [MCZC, MZSP]; Nova Teutônia, XI.1974, 300–500 m, 1 soldier, F. PLAUMANN [MZSP]; Rodeio, Dez. 1955, 1 worker, R. MUELLER [MZSP]; Porto Novo, 17.X.1926, 1 worker, 1 soldier, 1 gyne, B. RAMBO [MZSP]; Blumenau, Dez. 1953, 1 worker, R. MÜLLER [MZSP]. Rio Grande do Sul: no further locality, 3 workers, IHERING [MCSN], 1 worker (erroneously labelled as cotype of *jheringi*) [MHNG]; Laurentino, I.1958, 1 worker, R. MÜLLER [MZSP].

Fig. 337. *Cephalotes pallidicephalus* (Smith). Male from Itajaí (Santa Catarina), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

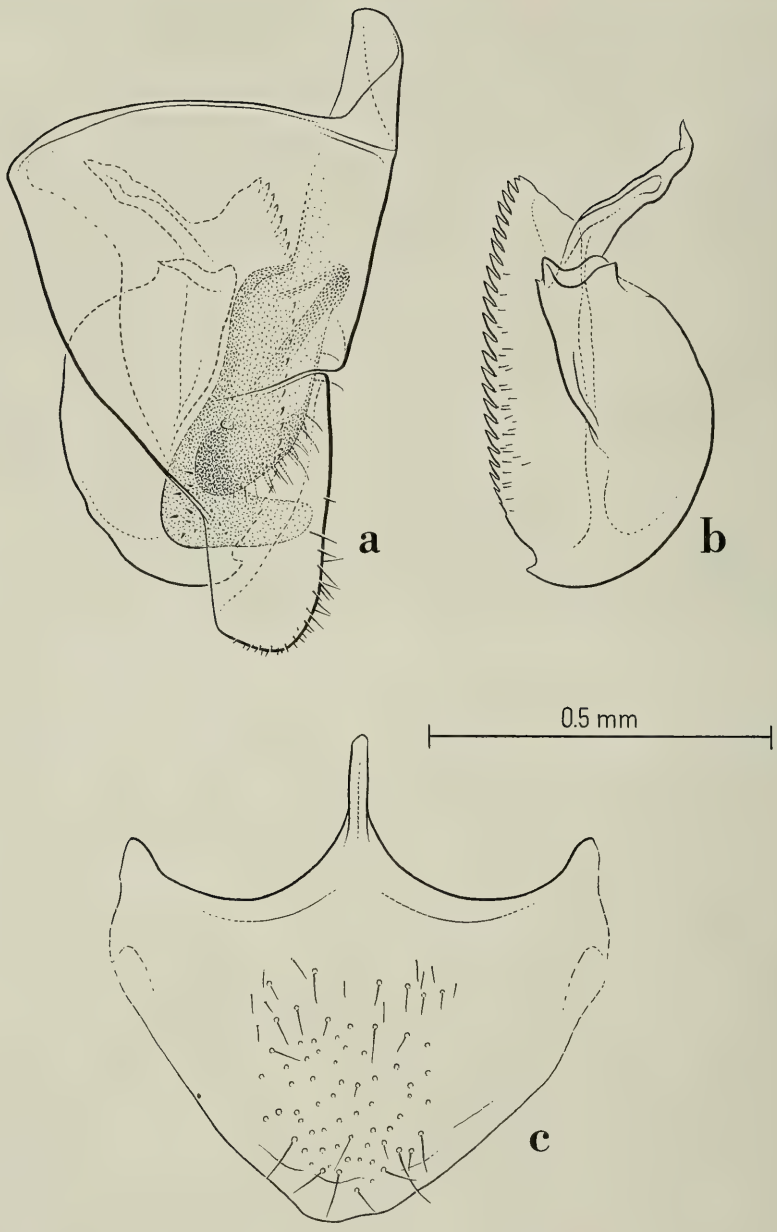


Fig. 338. *Cephalotes pallidicephalus* (SMITH). Male from Itajaí (Santa Catarina), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

Discussion. - *Pallidicephalus* has been described from Mexico without further locality. We regard the Mexican origin of this species (confirmed by the label of the holotype) as highly improbable. In fact, all the members of the *angustus* clade are confined to the central and southern part of S America extending up to Colombia in their northernmost range. All specimens we refer to *pallidicephalus* originate from south and central Brazil. KEMPF (1964), after examination of the holotype gyne of *pallidicephalus*, concluded its synonymy with *scutulatus* (SMITH 1867). We cannot agree with this proposal since *scutulatus* gynes (probably unknown to KEMPF) associated with workers in MCZC and MCSN differ greatly from the *pallidicephalus* holotype (and other specimens as well) at least in the following characters: angulate hind femora, ocelli distant from the border of the cephalic disc, humeral angles membranaceous, and broader petiolar and postpetiolar appendages. *Striativentris* is a straight synonym of *pallidicephalus*, though it would be difficult to blame EMERY for this error: the usual difficulties in recognising SMITH's species from his descriptions are even worsened in this case by the geographical error.

The worker of *pallidicephalus* is unique within *Cephalotes* for the thick, longitudinal striae on the first gastral tergite. The soldier and the gyne of *pallidicephalus* have a similar sculpture, but thinner and restricted to the sides of the tergite. Some soldiers of *notatus* and the gynes of *notatus* and *goeldii* converge with *pallidicephalus* for this character. The thickness of the gastral striation is subject to some individual variation but its size in *pallidicephalus* regularly exceeds the condition of any other known *Cephalotes* species. The shape of the gastral striation may also undergo limited variation in being convergent posteriorly and less regular in some specimens.

Distribution: Brazil.

Cephalotes notatus (MAYR) new combination
Figs. 339, 340

Cryptocerus notatus MAYR, 1866 b: 907, fig. 16. Gyne. Original description. Type locality: Brazil. Type material: holotype gyne in the NHRS (KEMPF, 1967: 367), cannot be located at present (B. GUSTAFSSON, personal communication 13.2.1996).

Paracryptocerus fleddermanni KEMPF, 1958 a: 87, pl. 2, fig. 3, pl. 3, fig. 4, pl. 5, fig. 1. Worker, soldier. Original description. Type locality: São Sebastião and Alto da Serra (San Paulo, Brazil). Type material: 2 workers, 1 soldier (holotype soldier and paratype workers) from São Sebastião (San Paulo, Brazil), B. FLEDDERMANN, 1 worker (paratype), same locality, 5.2.1953, W. W. KEMPF [all MZSP], examined. Synonymy by KEMPF, 1967: 367.

Paracryptocerus notatus (MAYR), KEMPF, 1958 a: 140. First combination in *Paracryptocerus*.

Zacryptocerus notatus (MAYR), BRANDÃO, 1991: 387. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *angustus* clade differing from its sister species, *goeldii*, in the worker, by the ventral face of the head longitudinally striate, and, in the soldier and gyne, by the foveae, irregular and more impressed.

Worker (Fig. 339) (description of KEMPF, 1958 a sub *fleddermanni*). - "Total length 3.7–4.2 mm; maximum length of head 1.07–1.21 mm; maximum length of thorax 1.03–1.18 mm. Black; the following ferruginous: tip of mandibles, tip of scape, basal funicular segments, tip of thoracic and peduncular teeth, tip of femora, all tarsites; pale testaceous: frontal carinae, anterolateral gastral crests and an irregular, narrow spot just inside of the crest, on the anterolateral gastral lobes; fuscous testaceous: edge of frontal carinae, tibiae.

Head subopaque, subquadrate; its maximum length slightly exceeding the interocular width (34:31; 30:28). Clypeal and frontal sutures vestigial. Lateral borders of head slightly

diverging caudad, straight, the posterior portions neither excised in front of, nor sinuate nor upturned above eyes. Occipital corners obliquely truncate, the inner corner obtuse. Occipital border gently emarginate. Dorsum of head a little convex, finely reticulate-punctate, more sparsely covered with squamiferous foveolae, which are more numerous and somewhat crowded toward the occipital border; frontal carinae flat, without conspicuous foveolae. Lower face of head longitudinally rugose, with sparse squamiferous foveolae anteromesially.

Thorax subopaque. Anterior border scarcely convex, nearly straight. Shoulders subrectangular. Lateral border of pronotum with two approximated triangular, slightly foliaceous teeth, followed by an irregularly edged foliaceous crest, which is either irregularly dentate or crenate, or exhibits another larger, yet blunt tooth; the posterior corner subrectangular. Promesonotal suture vestigial or absent. Mesonotum with a short pointed tooth, projecting from each side. Mesoepinotal suture slightly impressed laterally, absent in the middle. Lateral border of basal face of epinotum with three or four small teeth, and an additional denticle on the sides of the declivous face. The latter excavated in the middle. Dorsum of thorax finely reticulate-punctate, rather densely foveolate, especially on mesonotum, where the intervals between the crowded pits form a raised reticule of intertwining rugosities. Sides of thorax, including the laterotergites of pronotum, horizontally striato-rugose. Fore coxae with a few fine longitudinal rugosities.

Peduncular segments as in soldier, but the postpetiole is less strongly convex above, and lacks the distinct median triangular area.

Gaster subopaque, elliptical, longer than in *striativentris* (= *pallidicephalus*), strongly emarginate anteromesially, the anterolateral lobes with a narrow, transparent, thin border which does not reach backwards beyond the stigma of the first tergite, the sides of which are practically immarginate behind the spiracle. First tergite and sternite finely reticulate-punctate, the latter also with very fine and sparse longitudinal rugosities.

Standing hair on mandibles, clypeal border, funicular segments, apical border of gastral tergites and sternites II - IV, along the edge of the frontal carinae and lateral borders of head, none on the occipital corner. Squamiform, canaliculate, silvery, decumbent hair rather abundant in all foveolae of dorsum of body, more sparsely on frontal carinae, legs, lower face of head, sides of thorax, gastral sternites, where they are usually smaller and simple, not canaliculate."

Measurements (in mm) and indices: TL 3.66–4.56; HL 0.96–1.08; HW 1.00–1.20; EL 0.25–0.28; PW 0.85–1.06; PeW 0.47–0.53; PpW 0.52–0.61; HBaL 0.38–0.43; HBaW 0.08–0.10; CI 104.2–111; PI 113.2 –117.6; PPeI 108.8–200.0; PPpI 163.5–173.8; HBaI 21.0–23.2.

S o l d i e r (Fig. 340) (description of KEMPF, 1958 a sub *fleddermanni*). - "Total length 5.4 mm; maximum length of head 1.64 mm; maximum length of thorax 1.46 mm. Black; the following light brown or yellowish brown: sides of head, occipital lobes, floor of cephalic disc, dorsum of thorax, tip of postpetiolar spines, tip of femora; dirty testaceous: tibiae, the four gastral maculae, the latter infuscated and the anterior pair fused to each other; ferruginous: tip of mandibles, except for the chewing border, basal funicular segments, cheeks, the four apical tarsites. Cephalic disc and pronotum with an anteromedian black band. Mesoepinotum ferruginous to infuscated discad.

Head rather shiny; surmounted by a subcircular, somewhat elongate (46:43), deeply excavated, completely marginate disc. Lateral and posterior border of disc strongly raised and upturned, concealing the floor of the disc, when head is seen in profile. Anterior border of disc curved, its sides gently convex, its posterior border evenly rounded, not truncate. Clypeal sutures invisible. Floor of disc conspicuously concave laterally and behind, having a prominent anteromedian and caudad another yet more feeble convexity. In front of the anterior bulge, the floor of the disc abruptly slopes downward to the supramandibular excision, which is at a distinctly lower level than the rest of the disc. Occipital lobes sharply marginate and crested, their lateral border convex, converging caudad, their posterior border concave, both borders forming at their junction a prominent, apically rounded tooth. Floor of disc and sides of head coarsely foveolate, the diameter of the pits more than twice as large as the diameter of the raised, highly shining intervals, which form a network with large meshes. Above the antennal scrobe the floor of the disc is semitransparent and the foveolae are

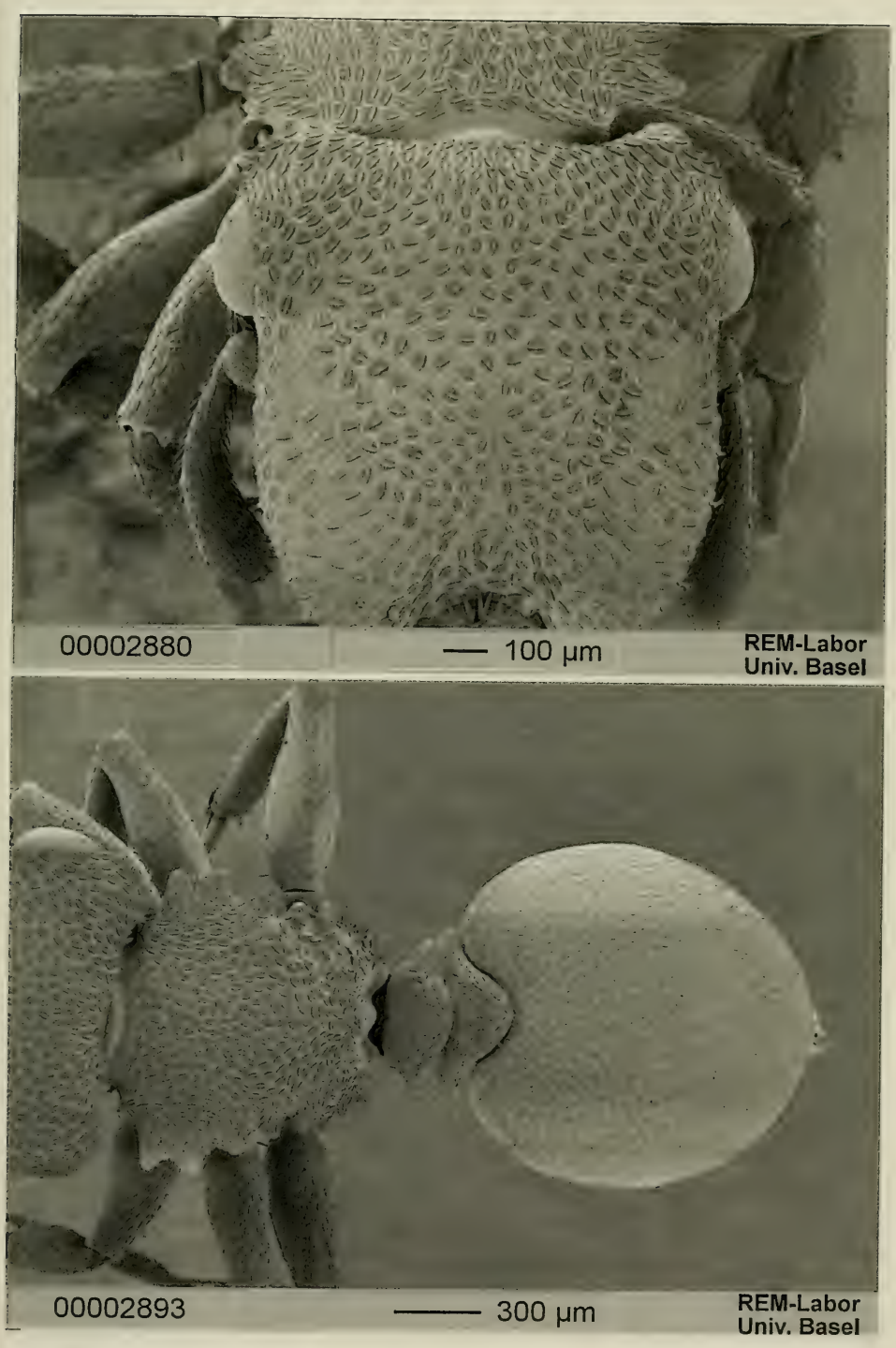


Fig. 339. *Cephalotes notatus* (MAYR). Worker from Caraguatatuba (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

transversely compressed, the intervals very distinct in the form of transverse rugosities. Lower face of head reticulate-rugose and sparsely foveolate discad, more or less longitudinally rugose posterolaterad.

Thorax rather shiny above, subopaque on sides and declivous face. Anterior border of pronotum straight in the middle, slightly oblique and concave laterally, the latter joining the former at a distinct very obtuse angle. Anterior corner of pronotum subdentate, the first half of the lateral borders subparallel, forming a thin, raised crest, which grades imperceptibly into the bisinuous, mesially not incised nor interrupted, but strongly crested transverse pronotal carina. Anterolateral portion of pronotum unusually excavate. Posterior half of borders of pronotum immarginate, sinuous, strongly converging caudad, forming a right angle at the posterior corner. Promesonotal suture vestigial. Sides of mesonotum with a projecting, strongly marginate, slightly crested, obliquely truncate lobe. Mesoepinotal suture complete and impressed. Basal face of epinotum transverse, its anterior corner subdentate, its sides with a more or less triangular lobe, its posterior corner with a tooth, similar to that of *striativentris* (= *pallidicephalus*), pointing upward, but scarcely laterad, being however feeble, not stout. Declivous face somewhat excavated with a prominent, sharply marginate border on each side. Dorsum of thorax reticulate-rugose and foveolate, the bottom of the pits being finely punctate. Foveolae much smaller and less regular than those of the cephalic disc, usually inconspicuous, especially on mesonotum where more or less transverse and crowded rugosities prevail. Sides of thorax finely and sharply reticulate-punctate. Laterotergite of pronotum reticulate-rugose above, longitudinally rugose below. Pleura with few, rather vanishing rugosities: Declivous face of epinotum finely reticulate-punctate, and finely and sparsely transversely rugose. Fore coxae reticulate-punctate.

Peduncular segments irregularly rugose and foveolate above, sides and lower face finely reticulate-punctate. Petiole somewhat narrower than postpetiole, its lateral teeth pointing obliquely caudad, its anterior face obliquely truncate and submarginate above. Postpetiole with the costumary curving spines, the tip of which is strongly recurved caudad. Anterior face first vertical than curving caudad to a horizontal position, forming a triangular submarginate area dorsally on the body of the postpetiole.

Gaster elliptical, emarginate anteromesially, its anterolateral lobes marginate yet not visibly crested. Both the first tergite and sternite are opaque, finely reticulate-punctate, the latter having also very fine and sparse longitudinal rugosities.

Standing hair, as usual, on mandibles, funiculus, and on tip of gaster. A fringe of sparse, thickish hair around the anterolateral edge of the cephalic disc reaching the anterior border of the eyes. Decumbent, squamiform, usually canaliculate, always glittering, silvery hair on lower surface of head, epinotum, sides of thorax, dorsum of peduncular segments, and first gas-tral tergite. From each of the very large pits on cephalic disc arises a minute, thick, curved hair; similar, yet more erect, and somewhat longer hair arises from the pits on promesonotum. Simple decumbent scalelike hair on legs and gastral sternite."

Measurements (in mm) and indices: TL 5.02–6.32; HL 1.32–1.56; HW 1.42–1.64; EL 0.29–0.32; PW 1.40–1.64; PeW 0.54–0.60; PpW 0.60–0.68; HBaL 0.40–0.44; HBaW 0.10–0.12; CI 102.8–107.6; PI 100.0–101.4; PPeI 240.0–282.7; PPpI 225.0–241.2; HBaI 25.0–27.3.

G y n e (description of KEMPF, 1958 a sub *fleddermanni*). - "Dealate. Total length 7.5 mm; maximum length of head 1.89 mm; maximum length of thorax 2.14 mm. Black; the following orange: sides of head, occipital lobes, floor of cephalic disc, except for the large central black area, shoulders; fuscous-ferruginous: mandibles, basal funicular segments, tarsites; testaceous: tibiae, especially the extensor face; the four gastral maculae are pale yellow; all crests inside of the orange-colored parts are light brown.

Resembling the soldier, with the differences of the caste. Cephalic disc more elongate (53: 43), deeply excavated, floor of disc invisible, when head is seen in profile. The posteromedian bulge of head disc scarcely distinguishable. Anterior depression behind the supramandibular excision as in soldier. Posterior ocelli removed from the occipital border. Two imaginary lines drawn from the anterior ocellus to each of the posterior ocelli form a right angle. The same characteristical occipital lobes as in soldier. Sculpture of head identical, except for the foveolae on floor of cephalic disc, which are more transverse, and the transverse raised rugosities more prominent, than the longitudinal ones. Thorax relatively elongate (length: width

Fig. 340. *Cephalotes notatus* (MAYR). Soldier from Caraguatatuba (São Paulo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

proportion 60:44). Anterior border of pronotum crenulate laterally, the anterior corner bluntly angulate and crested. Anterolateral excavation and transverse carina of pronotum similar to that of soldier. Lateral borders of pronotum straight, slightly converging caudad. Scutum and scutellum coarsely and densely reticulate-rugose, without clearly visible foveolae. Sides of basal face of epinotum with a rather rounded lobe. Posterior tooth pointing obliquely caudad, as in *striativentris* (= *pallidicephalus*). Mesopleural tooth present, not prominent. In front of this tooth the mesopleurae are vertically rugose, behind the tooth horizontally rugose. Peduncular segments as in figure, the lateral tooth of the petiole longer, more acute lacking a thin, drawn out tip, as frequently in *striativentris* (= *pallidicephalus*). Postpetiole with a middorsal triangular area as in soldier. Both the first gastral tergite and sternite opaque, finely yet sharply reticulate-punctate, the latter with dense fine longitudinal rugosities. Squamiform hair scarce or little apparent, that of gaster extremely small, visible only at high magnification, simple. Instead both on thorax, postpetiole and gastral tergite there are evenly scattered, short, standing hairs. The same also on the legs."

Measurements (in mm) and indices: TL 7.64–8.28; HL 1.72–1.76; HW 1.60–1.64; EL 0.32–0.36; PW 1.52–1.56; PeW 0.64; PpW 0.80–0.84; HBaL 0.56–0.57; HBaW 0.13–0.14; CI 90.9–95.3; PI 105.1–105.3; PPeI 243.7–250.0; PPpI 185.7–200.0; HBaI 22.8–25.0.

Material examined. - **Brazil**: Rio de Janeiro: Rio de Janeiro, Corcovado, 7.IX.1891, 1 worker, [ZSMC]; same locality, 10.XI.1958, 2 gynes, SEABRA & ALVARENGA [MZSP]; Represa Rio Grande, Guanabara, IV.1961, 1 soldier, F. M. OLIVEIRA [MZSP]. São Paulo: São Sebastião, 06.III.1958, 26 workers, 5 soldiers (determined as *fleddermanni*, some pins bear an additional label "topotypus and metatypus, W. W. Kempf") [MCZC, MZSP]; same locality, 30.I.1955, 2 workers, 1 soldier (holotype and paratype of *fleddermanni*), B. FLEDDERMANN [MZSP]; same locality, 5.II.1953, 1 worker (paratype of *fleddermanni*), W. W. KEMPF [MZSP]; same locality, 01.VII.1987, 500 m, 1 worker, C. R. F. BRANDÃO [MZSP]; same locality, 11.X.1990, 3 workers, M. L. DE ANDRADE [CPCC, NHMB]; Ilha dos Búzios, 18.X.1963, 10 workers, 6 soldiers, Exp. Dep. Zool. [MZSP]; Caraguatatuba, Res. Florestal, 40 m, 02.IV.1962, 32 workers, 5 soldiers, K. LENKO [MZSP]; Avaré, 14.IX.1974, 1 worker, L. LANE [MZSP]; ? Eldorado, 5.X.1990, 1 worker, M. L. DE ANDRADE [NHMB] (see the Discussion).

Discussion. - *Notatus* and *goeldii* differ from each other much more in the workers than in the soldiers and gynes. The presence of ventral cephalic striation, the vertexal lamellae narrower, and the spines of the petiole and postpetiole thinner are the main characters characterising the worker of *notatus* from that of *goeldii*. The soldier and the gyne of *notatus* and *goeldii* are very similar. Both species share synapomorphically the vertexal angles of the gynes and soldiers and the pronotal sides of the soldiers with broad, lamellaceous borders.

A single worker from Eldorado (São Paulo, Brazil) is very similar to *notatus* in body shape and sculpture, but differs from it by the frontal carinae upturned over the eyes, presence of dorsal petiolar denticles, the anterior fourth of the first gastral tergite reddish and the cephalic foveae broader and denser. We are convinced that this specimen represents a new species but prefer not to describe it until more material will be available.

Distribution: Brazil.

Cephalotes goeldii (FOREL) new combination
Figs. 341, 342, 343

Cryptocerus goeldii FOREL, 1912: 205. Worker. Original description. Type locality: Serra Vermelha (Rio de Janeiro, Brazil). Type material: Holotype worker (unique) in MHNG labelled: first label (red) "Typus"; second label (pink) "*Paracryptocerus goeldii* Forel, Holotypus, WWK"; third label "*Cr. Goeldii* Forel, Serra Vermelha, Prov. Rio, Göldi" (handwriting of FOREL); fourth label "Sp. *Cr. Goeldii*" (handwriting of Forel), fifth label "Coll. Forel" (printed); examined.

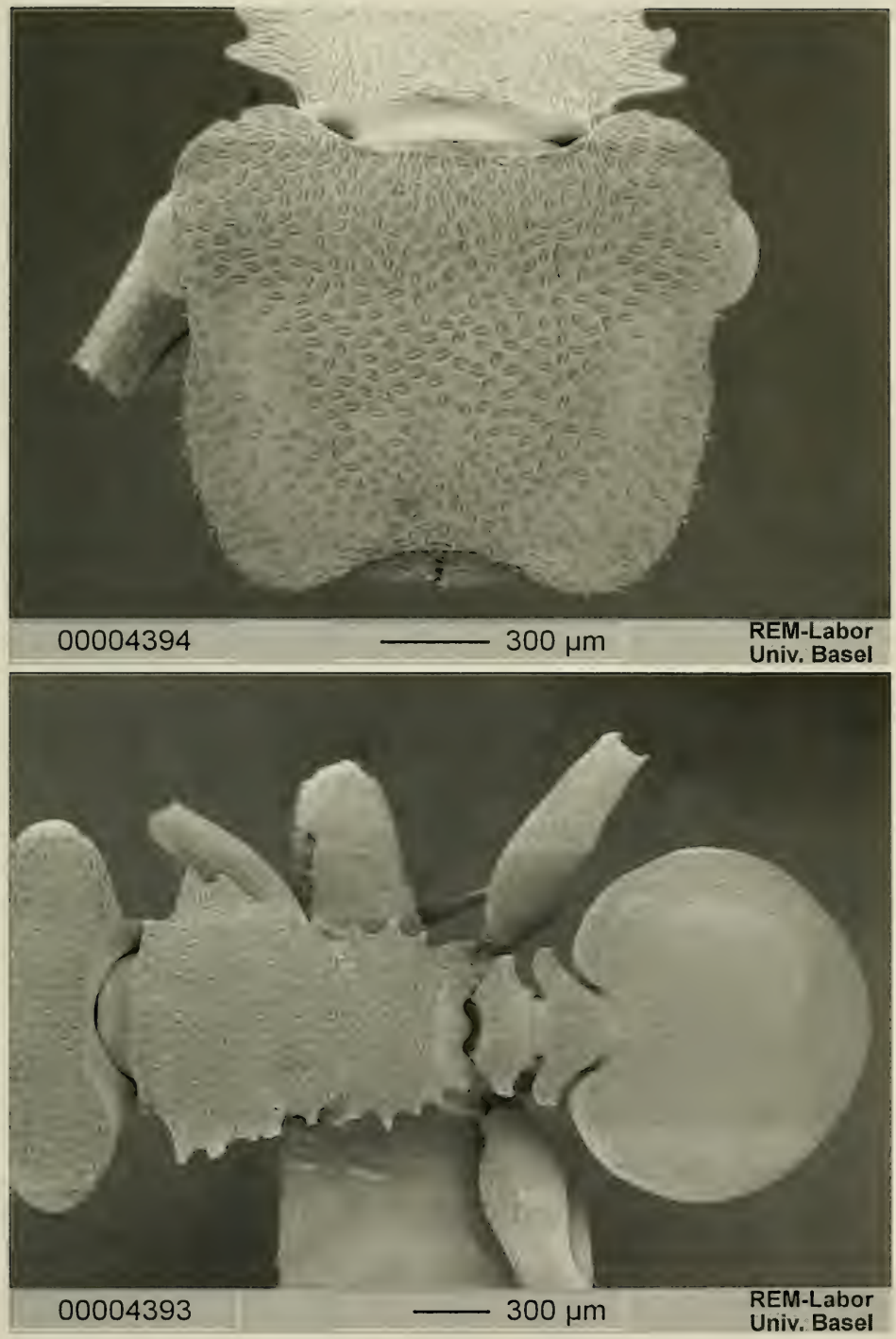


Fig. 341. *Cephalotes goeldii* (FOREL). Worker from Ilhéus (Bahia), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

Paracryptocerus goeldii (FOREL), KEMPF, 1958 a: 93. First combination in *Paracryptocerus*.
Paracryptocerus goeldii (FOREL), KEMPF, 1967: 366, fig. 3. Worker.
Zacryptocerus goeldii (FOREL), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

D i a g n o s i s . - A member of the *angustus* clade differing from its sister species, *notatus*, in the worker, by the ventral face of the head without longitudinal striae, and in the soldier and gyne, by the much more regular and less impressed foveolation.

W o r k e r (Fig. 341) (description of KEMPF, 1967). - "Total length 4.6 mm; maximum head length 1.36 mm; maximum width of head above eyes (the latter excluded) 1.39 mm; thorax length 1.39 mm; petiole width 0.58 mm; postpetiole width 0.64 mm; gaster width 1.49 mm.

The worker of this species shares with *angustus* and *striativentris* (= *pallidicephalus*) the unique feature (in the *angustus* group!) of having the gaster laterally sharply marginate well beyond the anterior half, the translucid anterolateral lamella extending backwards much beyond the distinctly visible dorsal stigma.

The differences from *angustus* are as follows: Tip of scape, tibiae and tarsi rather yellowish brown than ferruginous; gastral markings more extensive, a broad and well circumscribed band just lies inside the lateral border. Occipital lobes subhyaline, yellowish, conspicuous. Dentition of thoracic border somewhat different, principally on epinotum, where there are four distinct teeth. Promesonotal suture quite distinct (usually obsolete, sometimes vestigial in *angustus*). Lateral spines of pedicellar segments not needle-like but broader and flattened; those of postpetiole distinctly recurved. Petiole without antero-dorsal denticles; postpetiole dorsally completely flat. Gaster short, subcircular, with the anterolateral hyaline border broader than in *angustus*.

The differences from *striativentris* (= *pallidicephalus*) are as follows: color, occipital lobes and anterolateral border of gaster as stated under *angustus*. Sternum I of gaster without coarse costae or rugae but smooth."

Measurements (in mm) and indices: TL 4.00–470; HL 1.00–1.16; HW 1.24–1.42; EL 0.26–0.28; PW 0.92–1.12; PeW 0.49–0.56; PpW 0.52–0.62; HBaL 0.40–0.46; HBaW 0.11–0.13; CI 122.4–124.0; PI 125.0–134.8; PPeI 187.7–200.0; PPpI 174.2–183.6; HBaI 27.5–28.3.

S o l d i e r (Fig. 342) (previously undescribed). - Head very large, with a complete, round disc. Border of the disc strongly raised and lamellaceous. Vertexal angles with an obtuse, broad lamella continuing up to the eyes. Vertexal border concave and without margin. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a short, denticulate carinae just in front of the eyes. Eyes convex and partially hidden by the head disc.

Mesosoma. Anterior pronotal border gently convex. Pronotal sides with a pair of very broad expansions, anteriorly obtuse, medially truncate, posteriorly converging. Border of the pronotal expansions lamellaceous. Pronotal carina lamellaceous, strongly developed, narrowing from the sides to the center where it is interrupted by a superficial sulcus. Promesonotal suture impressed. Mesonotum with a broad, round tooth with lamellaceous border. Propodeal suture deeply impressed. Propodeum with well differentiate basal and declivous faces. Sides of the basal face with a small swelling followed by two pairs of teeth; first pair of propodeal teeth short, broad and rounded, the second pair broad, thick, curved upwards and forwards at the apex and obtuse. Declivous face concave in the middle; its sides converging and bearing a pair of short, lamellaceous teeth.

Petiole with differentiate anterior and posterior faces; anterior face truncate, posterior face sloping backwards. Sides of the petiole, medially, with a thick, round tooth directed backwards. Postpetiole convex. Postpetiolar sides with a pair of thick, round expansions arising from the anterior border and directed anterolaterally.

Gaster oval and with a pair of protruding, anterolateral lamellae reaching the stigma.

Mid and hind femora without angles or denticles. Hind basitarsi slightly more compressed apically than distally and with slightly broad base.

Sculpture. Head dorsum superficially punctate and covered by dense, shallow foveae more superficial and smaller on the anterior third. Ventral part of the head strongly punctate, with longitudinal, slightly irregular rugosities, thinner, more superficial and superimposed to

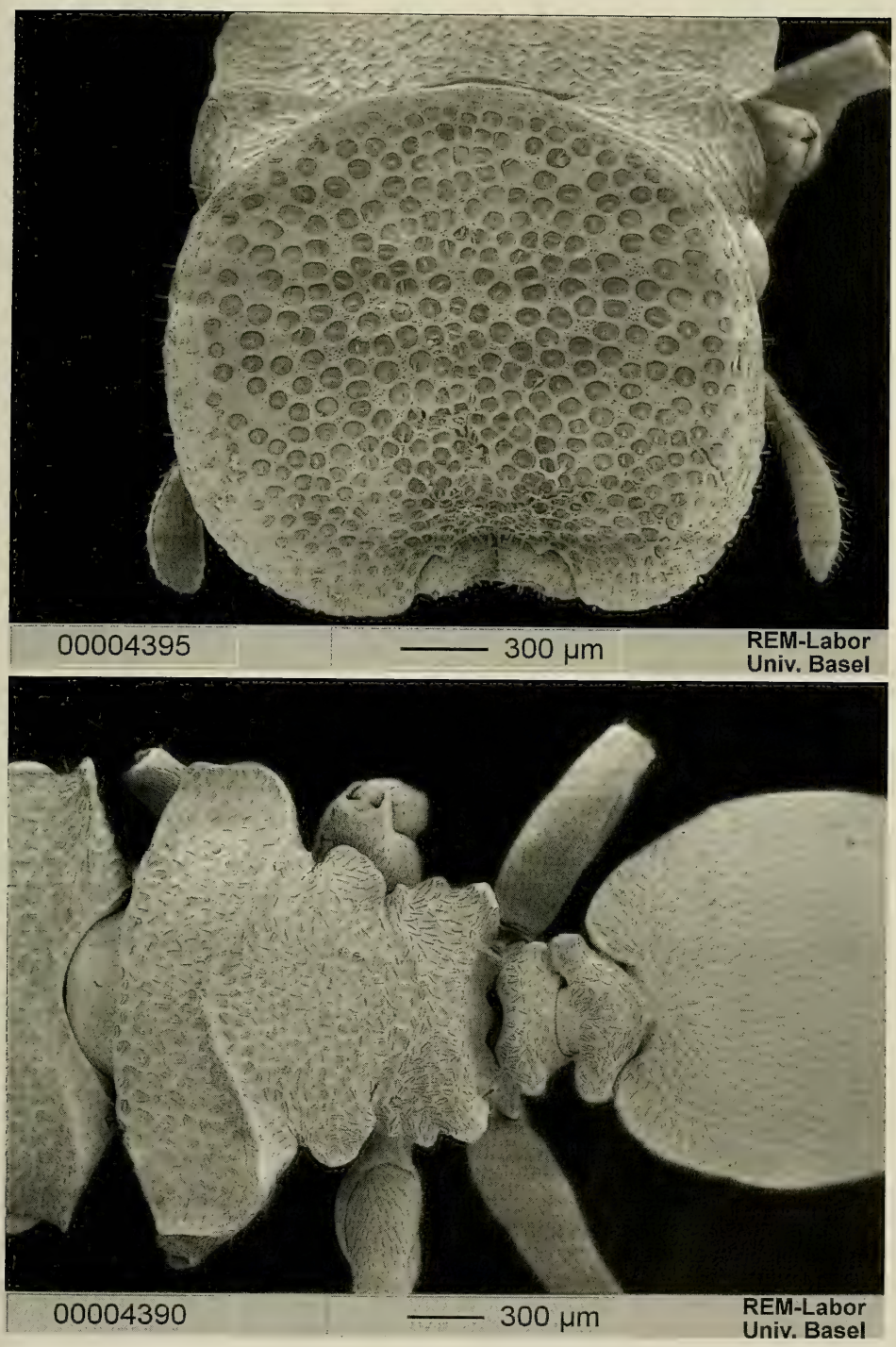


Fig. 342. *Cephalotes goeldii* (FOREL). Soldier from Linhares (Espírito Santo), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

irregular, shallow foveae on the anterior half. Sides of the head and mesosoma with the same type of sculpture as the head dorsum but with foveae more irregular and smaller on the basal face of the propodeum. Propleurae with the same type of sculpture as on the posterior half of the ventral part of head. Lower meso- and metapleurae and pedicel reticulate and with small, irregular foveae. Upper meso- and metapleurae, declivous face of the propodeum, gaster and legs reticulate. First gastral tergite with irregular, small, superficial, oval foveae on the anterior third only; two posterior thirds of the tergite and anterior third and sides of the sternite with thin, superficial, irregular rugulosities. Outer face of the femora and of the tibiae with superficial, oval foveae. Center of the posterior half of the first gastral sternite shining.

Pilosity. Each fovea of the head dorsum with a canaliculate-subclavate, suberect to decumbent hair; other body foveae with appressed, canaliculate hairs. Parts of the legs and of the gaster without foveae with the same appressed hairs as on the mesosoma, but thinner. Sides of the head disc, legs and posterior border of the tergites and sternites with suberect, sparse, clubbed hairs. Sternites with rare, long, pointed hairs.

Colour. Ventral part of the head, center of the mesosoma, pedicel and three ventral fourths of the pleurae brown; sides and dorsum of the head, sides of the mesonotum, last dorsal fourth of the pleurae, sides of the pedicel, yellow-orange. Legs and gaster dark orange-brown with lighter outer face of the tibiae and with a pair of long, yellowish strips on the sides of the first gastral tergite.

Measurements (in mm) and indices: TL 5.96; HL 1.64; HW 1.88; EL 0.32; PW 1.92; PeW 0.61; PpW 0.67; HBaL 0.43; HBaW 0.14; CI 114.6; PI 97.9; PPeI 314.7; PPpI 286.6; HBaI 32.5.

G y n e (previously undescribed). - Head subquadrate, longer than broad. Head disc less broad, less round and with the floor less concave than in the soldier. Sides of the disc with crenulate border. The rest as in the soldier.

Mesosoma. Anterior pronotal border straight and separate from the sides by a depression. Pronotal sides with a pair of narrow, obtuse, lamellaceous expansions narrowing posteriorly. Pronotal carina as in the soldier but lower. Mesonotum and scutellum flat in profile. Basal face of the propodeum with two pairs of teeth; the first pair small and triangular, the second one larger, pointed and directed backwards.

Petiole subquadrate, with the anterior face sloping and with the posterior one short and declivous. Petiolar sides with a pair of minute, triangular denticles. Postpetiole convex; postpetiolar sides with a pair of thick expansions arising from the anterior border, directed anterolaterally and with a pointed tip strongly curved backwards.

Gaster oval. Anterolateral gastral lobes protruding and with a thin, lamellaceous margin not reaching the stigma posteriorly.

Legs as in the soldier.

Sculpture. As in the soldier but differing in the following: body foveae more superficial and more regular on the mesosoma. Mesopleurae with small, irregular foveae. Metapleurae with irregular rugosities. Anterior third of the first gastral tergite without foveae but with superficial, longitudinal, slightly irregular, rugosities continuing backwards but less impressed; sides of the first gastral sternite with the same rugosities as on the anterior third of the tergite.

Pilosity. As in the soldier, but with the following differences: hairs originating from the cephalic foveae erect; clubbed hairs also on the mesosoma, pedicel and gaster. Parts of the gaster and of the legs without foveae with thinner hairs

Colour. Ventral part of the head, center of the floor of the disc and of the pronotum, mesonotum, propodeum, pedicel and gaster dark brown to black; sides of the head, of the floor of the disc and of the pronotum yellow-orange. Legs dark ferruginous to brown with yellow tibiae. Sides of the first gastral tergite with two pairs of broad, yellow spots, the first pair on the anterior third and the second one in the posterior third.

Measurements (in mm) and indices: TL 8.68–9.02; HL 1.88–2.00; HW 1.88–1.96; EL 0.34–0.38; PW 1.88–1.92; PeW 0.65; PpW 0.80–0.90; HBaL 0.61–0.63; HBaW 0.19; CI 98.0–100.0; PI 97.9–104.2; PPeI 289.2–295.4; PPpI 213.3–235.0; HBaI 30.1–31.1.

M a l e (previously undescribed). - Head (eyes included, mandibles excluded) about 2/3 broader than long. Vertexal angles straight and converging posteriorly. Ocelli large, extremely protuberant. Vertex convex. Frontal carinae simply marginate, diverging backwards and not

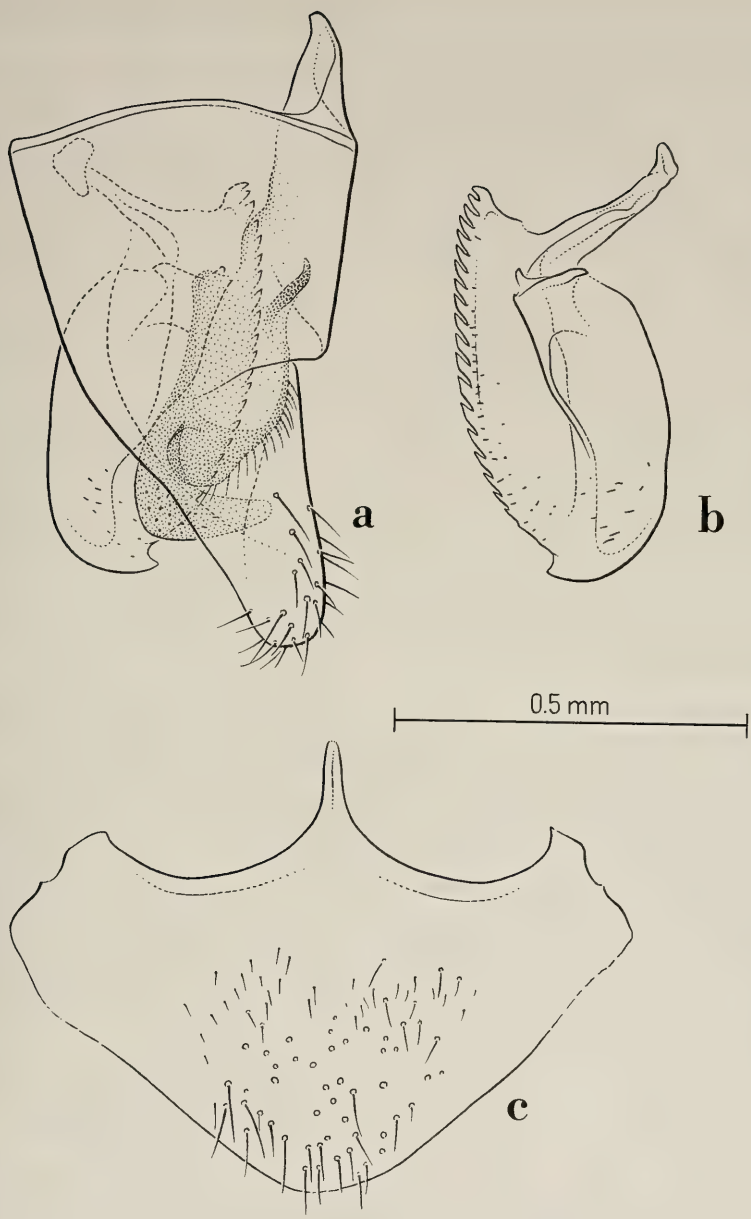


Fig. 343. *Cephalotes goeldii* (FOREL). Male from Ilhéus (Bahia), Brazil. Genital appendages: a) lateral view of the right parameres and of their relative positions; b) left aedeagus in profile; c) subgenital plate in ventral view.

reaching the posterior border of the eyes. Frons flat. Clypeus convex. Mandibles short and laterally carinate. Scapes thick, twice as long as the first funicular joint; remaining funicular joints thickening from the base to the apex.

Mesosoma narrower than the maximum head width (eyes included). Anterior pronotal border convex. Pronotal sides strongly diverging backwards and with a superficially marked margin. Mayrian and parapsidal furrows impressed. Propodeal sides converging posteriorly.

Anterior face of the petiole concave and laterally delimited by a pair of minute denticles. Sides of the petiole and of the postpetiole convex anteriorly and converging posteriorly.

Gaster slightly narrower than the mesosoma; its anterior border angulate.

Genitalia and subgenital plate as in Fig. 343.

Sculpture. Head, mesosoma and pedicel minutely reticulate-punctate and superficially foveolate, the foveae superimposed by very thin, slightly longitudinal rugosities on the vertex and on the frons and by irregular rugosities on the ventral part of the head; the foveae are larger and denser on the mesonotum and on the scutellum, rare or absent on the propodeum and on the pro- and metapleurae. Basal face of the propodeum with thick, irregular rugosities, longitudinal anteriorly and laterally, transversal in the middle. Pleurae with longitudinal rugosities thinner than those on the basal face of the propodeum, irregular on the meso- and on the metapleurae. Pedicel superficially reticulate and with sparse, very thin, longitudinal rugosities; sides of the petiole and postpetiole with rare, small, irregular foveae. Gaster, coxae and femora with superficial reticulation. Tibiae and tarsi punctate.

Pilosity. Body with long, erect hairs, denser on the head and on the mesosoma, subdecumbent on the posterior border of the gastral tergites, absent on the tibiae and tarsi. Gaster, tibiae and tarsi with short, appressed hairs, denser on the tibiae and tarsi.

Colour. Head, mesosoma, pedicel, first gastral tergite and sternite dark brown to black. Remaining gastral segments, coxae and proximal third of the femora brown. Remaining parts of the legs yellow.

Measurements (in mm) and indices: TL 4.68–5.50; HL 0.72–0.83; HW 0.86–1.00; EL 0.50–0.55; PW 0.86–1.00; PeW 0.34–0.38; PpW 0.35–0.43; HBaL 0.57–0.65; HBaW 0.07–0.08; CI 119.4–120.5; PI 113.6–114.7; PPeI 220.6–231.6; PPpI 204.6–214.3; HBaI 12.3.

Material examined. - **Brazil**: Bahia: Itabuna, 1 worker, 12.V.1971, J. A. Windler leg. [MZSP]; same locality, CEPLAC, 10.VIII.1992, 1 gyne, Ivan [CPCC]; Ilhéus, 20.IV.1993, 2 workers, Eduardo [CPCC]; same locality, 23–24.IV, 11.IX.1987, 2 males [CPCC]; same locality, CEPEC, 08.IV.1987, 03.III & 01.VI.1988, 3 males, P. Terra [CPCC]; same locality, 21.VIII.1992, 3 males, J. H. C. Delabie [CPCC]; same locality, 06.III.1995, 1 worker, 1 gyne, A. L. E. Souza [CPCC]; same locality, 07.III.1996, 1 male, J. H. C. Delabie [CPCC]; Cumuruxatiba, 16.II.1994, 1 male, P. A. O. Soares [CPCC]. Espírito Santo: Linhares, IX.1972, 1 male, M. Alvarenga [MZSP]; Linhares, Fazenda União. 12.IX.1991, 1 soldier, B. Conceição [CPCC]. Rio de Janeiro: Serra Vermelha, 1 worker (holotype), Göldi [MHNG].

Discussion. - *C. goeldii*, previously know only from the worker, had been considered close to *angustus* and *striativentris* (= *pallidicephalus*) in possessing semitransparent gastral lamellae extending to the end of the gaster as a thin margin. The discovery of the soldier and of the gyne, however, shows that *goeldii* is closer to *notatus*. *C. goeldii* shares synapomorphically with *notatus* the following worker characters: the propodeal sides with 4–5 denticles and the secondary loss of dorsal petiolar denticles. The soldiers of the two species share also the high lamella on the border of the disc, on the vertexal angles and on the pronotal sides. The gynes of the two species are also very similar and can be distinguished essentially by the foveae, more regular in *goeldii* than in *notatus*. Both species are sympatric in the SE coast of Brazil.

There is some individual variability in the number of lateral propodeal denticles which may be four or five, according to the specimen.

Our description of the male of this species is presumptive since none of the males we studied has been associated with workers or soldiers. We attribute these males to *goeldii* since they come from the same area from which *goeldii* is known. Other potential *Cephalotes* species of the same size and reported from the same area from which these males have been collected are *angustus*, *pallidicephalus* and *depressus*. The males of all these species are known and different from those described here. The males described here could be tentatively attributed to *C. notatus* as well (the male of which is unknown) but no *notatus* material is known from the states of Bahia and Espírito Santo where the males described here have been collected.

Distribution: Brazil.

Cephalotes frigidus (KEMPF) new combination
Fig. 344

Paracryptocerus adolphi (EMERY), KEMPF, 1958 a: 87, pl. 1, fig. 3, nec fig 5 (= *adolphi*) (nec EMERY, 1905). Misidentification.

Paracryptocerus frigidus KEMPF, 1960: 440, fig. 19. Worker. Original description. Type locality: Cabo Frío (Rio de Janeiro, Brazil). Type material: 1 worker (holotype), in Instituto Biológico, São Paulo, not available for the present study.

Zacryptocerus frigidus (KEMPF), BRANDÃO, 1991: 386. First combination in *Zacryptocerus*.

Zacryptocerus. BOLTON, 1994: figs. 216, 217. Worker. Tentative attribution.

Diagnosis. - A member of the *angustus* clade differing from *adolphi* and *dentidorsum*, in the worker, by the second pair of pronotal teeth lamellaceous and flat instead of solid and turned upwards.

Worker (Fig. 344) (description of KEMPF, 1960). - "Total length 3.9 mm; maximum length of head 1.14 mm; maximum width of head in front of the eyes 1.08; maximum diameter of eyes 0.29 mm; Weber's length of thorax 1.10 mm; maximum width of gaster 1.16 mm. Black, mandibles, antennae, legs except fore coxae, tips of occipital lobes, thoracic and pedicellar spines brown or ferruginous; frontal carinae and anterolateral foliaceous border of gaster testaceous.

Head subopaque, subquadrate. Mandibles finely and densely reticulate-punctate, opaque. Clypeal suture vestigial. Frontal carinae flat, depressed, semitranslucid, superficially reticulate-punctate above without conspicuous foveolae; borders anteriorly vestigially crenulate; lateral borders rather straight, evenly converging cephalad. Sides of head slightly but distinctly emarginate in front of eyes, convex and somewhat upturned above eyes. Occipital lobes with obliquely truncate and feebly crenate crest. Eyes very prominent, remarkably convex. Disc of cephalic dorsum moderately convex in both directions, front, vertex and occiput densely and finely reticulate-punctate, with sparser, larger, sharply impressed oval foveolae. Cheeks more heavily shagreened, with irregular rugulae and indistinct foveolae, lower border marginate. Gular surface reticulate-punctate with fine and sparse longitudinal rugulae.

Thorax subopaque, reticulate-punctate. Scapular corner free, angulate and subdentate. Lateral margin of pronotum tridentate, the first tooth acute, the following two teeth obtuse to blunt at apex. Promesonotal suture obsolete. Mesonotum at each side with a blunt to slightly bifid projecting tooth. Mesoepinotal suture practically absent, indicated laterally by a faint depression. Lateral margin of epinotum with 3 to 4 teeth, the anterior pair acute, the second the largest, the following 1–2 teeth minute, none at the bottom of the declivous face. Basal face of epinotum grading into declivous face. Dorsum of thorax reticulate-rugose and densely foveolate. Laterotergite of pronotum with a few horizontal costae. Remainder of sides of thorax longitudinally rugose and foveolate. Fore coxae laterally transversely costate. All legs subopaque and finely reticulate-punctate. Femora spindle-shaped. Tibiae not prismatic.

Petiolar and postpetiolar nodes with a prominent, drawn out spiniform appendage at each side. Postpetiole slightly broader than petiole. Body of petiole with an anterior subvertical

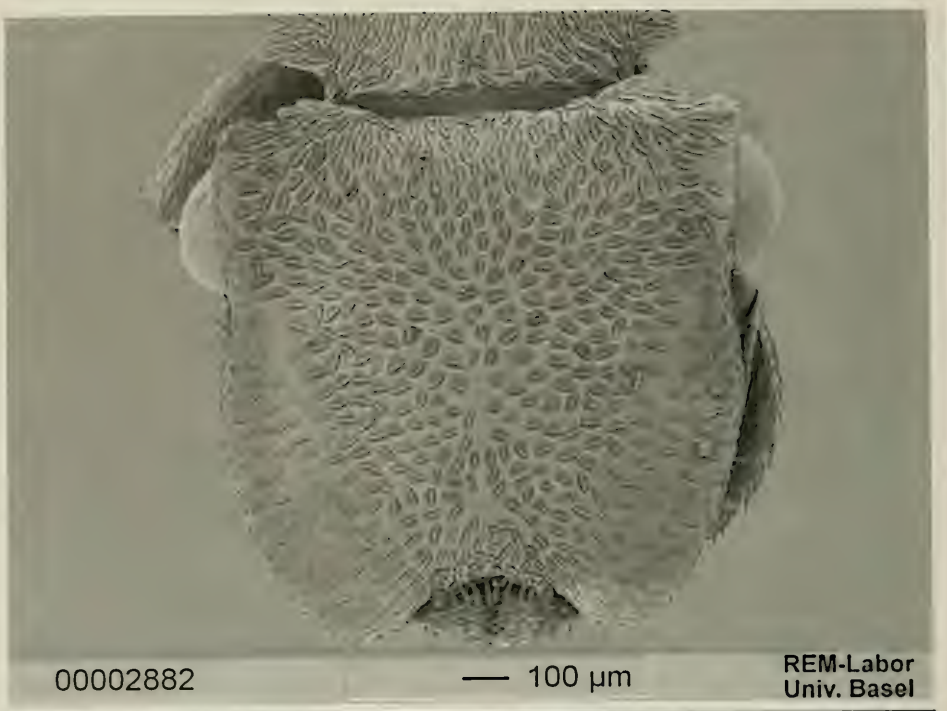


Fig. 344. *Cephalotes frigidus* (KEMPF). Worker from Pedra Azul (Minas Gerais), Brazil: head (top) and meso- and metasoma (bottom) in dorsal view.

truncate face, separated laterally from dorsal face by a faint and short transverse carinule. Postpetiolar dorsum in profile feebly convex. Both pedicellar segments subopaque, reticulate-punctate, and indistinctly reticulate-rugose.

Gaster broad oval, reticulate-punctate, subopaque, with super-imposed fine longitudinal but frequently anastomosing rugulae. Anterolateral foliaceous border subhyaline, relatively narrow, terminating posteriorly at the level of the first gastral spiracle.

Erect hairs scarce. Short, apically blunt setae anterolaterally on rim of frontal carinae, and on sides of head behind the eyes and in front of occipital corner. Longer and more pointed hairs on apex of gaster, including the anterior margin of the first tergite. Squamiform, canaliculate, silvery appressed hairs rather abundant in all foveolae on dorsum of body, more sparsely on frontal carinae, gular face, legs and posterior half of gaster, where they are narrower, simple and usually not canaliculate."

Measurements (in mm) and indices: TL 3.84–4.14; HL 0.98–1.04; HW 1.04–1.16; EL 0.27–0.29; PW 0.92–1.00; PeW 0.59–0.63; PpW 0.64–0.68; HBaL 0.32–0.34; HBaW 0.09; CI 106.1–111.5; PI 113.0–116.0; PPeI 155.9–158.7; PPpI 143.7–147.0; HBaI 26.5–28.1.

S o l d i e r (previously undescribed). - Head subquadrate, almost as broad as long, with a complete disc. Floor of the disc oblique on the anterior third and flat posteriorly. Border of the disc moderately raised and lamellaceous. Vertexal angles obtuse and bearing a broad lamella continuing up to the eyes. Mandibles with a strong carina. Dorsal border of the antennal scrobes with a short denticulate carina just in front of the eyes. Eyes convex and largely hidden by the disc.

Mesosoma. Scapular angles visible and short. Anterior pronotal border subtruncate. Pronotal sides with a pair of broad expansions, anteriorly obtuse, medially truncate, posteriorly strongly converging. Border of the anterior half of the pronotal expansions lamellaceous. Pronotal carina lamellaceous, strongly developed, thickening medially from the sides; medially the lamella is interrupted by a superficial sulcus. Promesonotal suture impressed. Mesonotum with a broad, round tooth with lamellaceous border. Propodeal suture deeply impressed. Propodeum with well differentiate basal and declivous faces. Sides of the basal face diverging posteriorly, with a pair of small, triangular teeth followed by another pair of large teeth curved upwards and forwards at the apex. Declivous face concave in the middle; its sides converging posteriorly.

Anterior face of the petiole separate from the posterior one by a thin, transversal carina; anterior face truncate and superficially concave medially; posterior face sloping backwards. Sides of the petiole with a pair of thin, pointed, medial teeth directed backwards. Postpetiolar node acuminate. Postpetiolar sides with a pair of thick, round expansions arising from the anterior border, directed anterolaterally and pointed backwards.

Gaster oval and with a pair of broad, anterolateral lobes.

Mid and hind femora without angles or denticles. Hind basitarsi slightly more compressed apically than distally and with a broader base.

Sculpture. Head dorsum superficially punctate and covered by contiguous, deep, irregular foveae, smaller on the anterior third. Ventral part of the head punctate-foveolate, the foveae deeper, denser and larger on the postero-lateral parts. Mesosoma with the same type of sculpture as the posterior part of the head dorsum, but with more regular, shallower, and smaller foveae on the basal face of the propodeum. Pleurae, pedicel, outer face of the femora and of the tibiae reticulate and with small, very superficial, oval foveae, absent on the metapleurae, larger on the pro- and mesopleurae. Gaster and remaining parts of the legs reticulate.

Pilosity. Each fovea of the head dorsum with a canaliculate-subclavate hair, suberect on the two posterior thirds and decumbent on the anterior third; other body foveae with appressed, canaliculate hairs of size proportional to the one of the fovea from which they originate. Other parts of the legs and of the gaster with the same appressed hairs as the mesosoma, but thinner, denser on the first gastral sternite. Sides of the head disc, pedicel, legs and posterior border of the tergites and sternites with suberect, rare, clubbed hairs.

Colour. Ventral part of the head, center of the mesosoma, two ventral thirds of the pleurae, pedicel, gastral sternites, coxae, two proximal thirds of the femora, and tarsi brown-black;

sides and dorsum of the head, sides of the mesonotum, last dorsal third of the pleurae, peduncular spines and remaining parts of the legs yellow-orange. First gastral tergite yellow and with the following parts dark brown: latero-ventral and posterior borders and a central, dorsal inverted triangle.

Measurements (in mm) and indices: TL 6.52; HL 1.80; HW 1.84; EL 0.35; PW 1.76; PeW 0.82; PpW 0.86; HBaL 0.43; HBaW 0.13; CI 102.2; PI 104.5; PPeI 214.6; PPpI 204.6; HBaI 30.2.

G y n e (previously undescribed). - Differing from the soldier in the following details:

Anterior third of the head less oblique than in the soldier. Sides of the disc with superficially crenulate border. Eyes largely visible in dorsal view. Humeral angles with a pair of short, triangular, lamellaceous expansions. Pronotal sides straight. Pronotal carina less high. Mesonotum and scutellum slightly convex in side view. Basal face of the propodeum with two pairs of teeth, the first pair small and triangular, the second one larger, subpointed and directed backwards. Petiole subquadrate, without transversal carina; anterior face of the petiole sloping and the posterior one short and declivous. Petiolar sides with a pair of minute, pointed denticles. Postpetiole less acuminate, more convex and with a short U-shaped carina; lateral expansions of the petiole smaller.

Gaster oval. Anterolateral gastral lobes protruding and with a very thin margin not reaching the stigma posteriorly.

Sculpture. Similar to the one of the soldier except: anterior half of the ventral part of the head with, sparse, irregular, longitudinal rugosities; foveae more superficial and more regular on the mesosoma; pleurae with longitudinal rugosities, thicker on the propleurae, transversal on the upper metapleurae, absent on the upper mesopleurae; upper mesopleurae densely covered by small foveae; coxae with rugosities, transversal on the fore coxae and longitudinal on the mid and hind coxae; anterior third of the first gastral tergite with superficial, very thin, longitudinal, slightly irregular rugosities; sides of the first gastral sternite with irregular, very thin and superficial rugosities.

Pilosity. As in the soldier but with the following differences: clubbed hairs denser and also present on the mesosoma and on the gaster. First gastral sternite with sparser thin, hairs.

Colour. Ventral part of the head, mesosoma, pedicel, gaster and coxae black; sides of the head, of the floor of the disc and of the pronotum yellow-orange; center of the disc and clypeus light brown. Two proximal thirds of the femora and tarsi brown. Remaining parts of the legs yellow. Sides of the first gastral tergite with two pairs of broad, yellow spots, the first pair in the anterior third and the second one in the posterior third.

Measurements (in mm) and indices: TL 7.56; HL 1.62; HW 1.60; EL 0.34; PW 1.56; PeW 0.66; PpW 0.79; HBaL 0.49; HBaW 0.15; CI 98.8; PI 102.6; PPeI 236.4; PPpI 197.5; HBaI 30.6.

M a t e r i a l e x a m i n e d . - **Brazil**: B a h i a : Santo Amaro, ESOMI, 12.XI.1987, 3 workers, E. FERRAZ [CPCC]. M i n a s G e r a i s : Pedra Azul, XI.1972, 800 m, 2 workers, SEABRA & ALVARENGA [MZSP]. R i o d e J a n e i r o : Represa Rio Grande, Guanabara, 2–6.IX.1960, 1 soldier, F. M. OLIVEIRA [MZSP]; same locality, IV.1961, 1 gyne, F. M. OLIVEIRA [MZSP].

D i s c u s s i o n . - We attribute to this species the soldier and the gyne described above with few doubts because of their similarities to the previously known worker, particularly in the shape of the petiolar nodes.

C. frigidus and its closest relatives *adolphi* and *dentidorsum* are well differentiated from the other members of the *angustus* clade by the long, thin spines of the petiole and of the postpetiole. The soldier of *frigidus*, the sole soldier known of the three previously mentioned species, shares with its next three outgroup species (*goeldii*, *notatus* and only some specimens of *pallidicephalus*) the broad vertexal lamella.

D i s t r i b u t i o n : Brazil.

Cephalotes adolphi (EMERY) new combination

Cryptocerus adolphi EMERY, 1905: 172, fig. 33. Worker. Original description. Type locality: Coxipó (Mato Grosso). Type material a worker (holotype) labelled "Coxipú, IX.900, typus", in MCSN, examined.

Paracryptocerus adolphi (EMERY), KEMPF, 1958 a: 86, pl. 1, fig. 5, nec fig 3 (= *frigidus*). Partim. First combination in *Paracryptocerus*.

Zacryptocerus adolphi (EMERY), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

Diagnosis. - A member of the *angustus* clade differing from its sister species, *dentidorsum*, in the worker by the less shining body, opaque and with more impressed sculpture; the difference between the two microsculptures is particularly impressive on the gaster.

Worker. - Head gently convex above, broader than long. Frontal carinae diverging backwards, incised in front and upturned above eyes. Vertexal angles bearing a subtruncate, broad, superficially crenulate lamella. Vertexal margin concave and marginate. Clypeal suture superficially impressed. Mandibles with a thin, short lateral carina.

Mesosoma declivous posteriorly. Scapular angles visible in dorsal view. Pronotal sides with a pair of pointed, triangular teeth followed by a pair of broad, stout, triangular lobes pointed upwards; apex of the pronotal lobes pointed and with a third minute denticle posteriorly. Promesonotal suture superficially impressed on the sides. Propodeum sloping backwards, with weakly differentiate basal and declivous faces; declivous face superficially concave in the middle and as long as the basal one. Propodeal sides with 4 pairs of pointed denticles, the first and the third pairs subequal and shorter, the second pair much longer, the fourth pair minute.

Petiole with oblique anterior face, with a pair of denticles dorsally and a pair of long, pointed, spines laterally. Postpetiole slightly broader than petiole; its node gently convex; postpetiolar spines long, thin, directed forwards at the base and curved at the apex.

Gaster oval. Anterolateral gastral border with a semitransparent lamella not surpassing the stigma posteriorly.

Hind femora without angles or denticles. Mid and hind basitarsi with subparallel sides.

Sculpture. Head dorsum minutely punctate and covered by small, round, superficial, variably clumped foveae, absent on the frontal carinae. Ventral part of the head superficially and minutely reticulate and with shallower, oval foveae on the anterolateral parts. Mesosoma, pleurae, pedicel, outer face of the femora and of the tibiae minutely and superficially punctate and with dense, oval foveae, sparser on the pleurae, shallower on the pedicel, on the outer face of the femora and of the tibiae. First gastral tergite with deep reticulation and covered by dense, superficial, oval foveae similar to those of the mesosoma but smaller. Remaining gastral segments and parts of the legs reticulate, the reticulation absent on the posterior half of the first gastral sternite.

Pilosity. Each fovea with an appressed canaliculate hair. Mandibles, border of the frontal carinae, sides of the postpetiole, posterior half of the first gastral tergite, and legs with rare, suberect, subclavate hairs. Posterior border of the gastral tergites and sternites with truncate hairs, rare on the sternites. Sternites with long, sparse, pointed hairs.

Colour. Light brown lighter on the frontal carinae, on the anterior third of the first gastral tergite, on the femora and on the tibiae.

Measurements (in mm) and indices: TL 4.00; HL 1.04; HW 1.26; EL 0.32; PW 0.95; PeW 0.64; PpW 0.68; HBaL 0.40; HBaW 0.08; CI 121.1; PI 132.6; PPeI 148.4; PPpI 139.7; HBaI 20.0.

Material examined. - **Brazil**: Mato Grosso: Coxipó, IX.1900, 1 worker (holotype) [MCSN]; Sinop, 55°37' W, 12°31' S, X.1974, 1 worker, M. ALVARENGA [MZSP].

Discussion. - This rare species is known on two workers only: the holotype from Coxipó and a second one collected recently not very far from the type locality. Actually, there are two localities called Coxipó in Mato Grosso, both

very close to the capital Cuiabá and ca. 15 km distant from each other: Coxipó do Ouro and Coxipó da Ponte. We ignore in which Coxipó our specimen has been collected. KEMPF (1960) redescribed what he believed to be *adolphi* (of which he did not see the type) on the basis of a Peruvian worker. After examining the type of *adolphi* and the Peruvian specimen studied by KEMPF, we decided to separate it specifically from *adolphi* under the name of *dentidorsum*. If, on one hand, separation of the two species is greatly facilitated by their direct comparison, the separation of these two from the other members of the *angustus* clade is easy for their sharing the superficial reticulation of the ventral face of the head and a unique synapomorphy (char. 31, state 1): the second pronotal tooth broadly lobate.

Distribution: Brazil (Mato Grosso).

Cephalotes dentidorsum DE ANDRADE n. sp.

Paracryptocerus adolphi (EMERY), KEMPF, 1960: 439, figs. 20–21. Worker. Nec EMERY, 1905. Misidentification.

Holotype: worker (unique), Peru, Valle Chanchamayo, 800 m, 1.VIII.1939, Weyrauch [MZSP].

Derivatio nominis: the species is named from the Latin *dens* (= tooth) and *dorsum* (back), referred to the characteristic pronotal spines.

Diagnosis. - A member of the *angustus* clade differing from its sister species, *adolphi*, in the worker by the gaster very shining and smooth instead of opaque and sculptured.

Worker (description of KEMPF, 1960, sub *adolphi*). - "Total length 3.9 mm; maximum length of head 1.20 mm; maximum width of head in front of the eyes 1.23 mm; maximum diameter of eyes 0.29 mm; Weber's length of thorax 1.12 mm; maximum width of gaster 1.12 mm. Light ferruginous; frontal carinae, occipital lobes, tips of thoracic and pedicellar spines, extensor face of tibiae testaceous.

Head subquadrate, supopaque, slightly broader than long. Mandibles finely and densely punctate, opaque. Clypeal suture vestigial. Frontal carinae semitranslucid, weakly sculptured throughout, nearly smooth and shining; their anterior border feebly crenulate. Sides of head excised in front of eyes, conspicuously upturned above eyes. Occipital lobes semitranslucid, foliaceous, with irregularly crenate border. Disc of cephalic dorsum notably convex in both directions. Upper surface of head finely, densely yet not heavily reticulate-punctate, somewhat shining, with rather large oval foveolae. Cheeks marginate below, more heavily shagreened, opaque, densely foveolate. Gular surface practically devoid of sculpture, quite shining.

Thorax conspicuously narrower than head, finely reticulate-punctate, the microsculpture superficial to obsolescent on dorsum which therefore is quite shining, heavier on sides which are opaque. Scapular corner free, angulate, and subdentate. Sides of pronotum anteriorly with a prominent spiniform tooth, followed by a broad, apically rounded, and conspicuously upturned lobe. Promesonotal suture obsolete. Mesonotum at each side anteriorly with a short tooth. Mesoepinotal suture more or less vestigial, not impressed. Basal face of epinotum grading into declivous face; their lateral border anteriorly with a small tooth, followed by a prominent spiniform tooth, and, farther down the declivous face, two more or less vestigial denticles. Dorsum of thorax with rather curved, elongate oval foveolae. Laterotergite of pronotum longitudinally costate. Rest of sides with elongate, horizontal foveolae. Legs subopaque, weakly shagreened. Femora spindle-shaped. Tibiae not prismatic.

Petiolar and postpetiolar nodes with a prominent spiniform appendage at each side. Dorsum of petiole with a pair of minute denticles. Dorsum of body of postpetiole, as seen in profile, moderately convex. Gaster short, oval, with obsolescent microsculpture, with broad, well-developed, hyaline lamellate anterolateral crests. Setigerous foveolae not developed.

Erect hairs scarce, a row of short, club-shaped setae along the rim of the frontal carinae and the sides of head back to the occipital angle. Longer, rather pointed setae on apex of gaster. Ground pilosity consisting of pale golden, appressed scale-like setae, sparsely covering the body and appendages of the insect. These scales are more conspicuous and distinctly canaliculate when lying in the foveolae of the dorsum and cheeks of head and on the thorax. Scales of gaster simple, finer, and not lying in foveolae."

Measurements (in mm) and indices: TL 4.00; HL 1.00; HW 1.20; EL 0.30; PW 0.91; PeW 0.62; PpW 0.66; HBaL 0.40; HBaW 0.08; CI 120.0; PI 133.3; PPeI 148.6; PPpI 137.9; HBaI 20.0.

Material examined. - **Peru:** Valle Chanchamayo, 800 m, 1.VIII.1939, 1 worker (holotype), WEYRAUCH [MZSP].

Discussion. - *C. dentidorsum* is described from a single specimen already used by KEMPF (1960) to re-describe what he thought to be *adolphi*. The complete lack of gastral microsculpture in *dentidorsum* allows separation of this species at glance from *adolphi*. The discrepancy between the specimen examined by KEMPF and the description of *adolphi* given by EMERY had been already noted by KEMPF (1960) himself.

Distribution: Peru.

5.7. *Cephalotes* incertae sedis

Cephalotes argentatus (SMITH) new combination

Cryptocerus argentatus SMITH, 1854: 218, pl. 19, fig. 7. Gyne. Original description. Type locality: Colombia. Type material: presumably lost (neither in the BMNH, nor in OXUM).

Paracryptocerus argentatus (SMITH), KEMPF, 1951: 232. First combination in *Paracryptocerus*.

Zacryptocerus argentatus (SMITH), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

Distribution: Colombia. Known only from the original description.

Cephalotes dorbignyanus (SMITH) new combination

Cryptocerus D'Orbignyanus (sic) SMITH, 1854: 218, pl. 19, fig. 5. Gyne. Original description. Type locality: S America. Type material: presumably lost (neither in BMNH, nor in OXUM).

Paracryptocerus dorbignyianus (sic) (SMITH), KEMPF, 1951: 232. First combination in *Paracryptocerus*.

Zacryptocerus dorbignyanus (EMERY), BRANDÃO, 1991: 387. First combination in *Zacryptocerus*.

Discussion. - According to ROGER (1861: 173) this species should be a straight synonym of *C. pavonii*.

Distribution: South America. Known only from the original description.

Cephalotes haemorrhoidalis (LATREILLE) new combination

Formica haemorrhoïdalis (sic) LATREILLE, 1802 b: 276. Worker. Original description. Type locality: Santo Domingo (Dominican Republic). Type material: not available for the present study.

Cryptocerus haemorrhoidalis (LATREILLE), LEPELETIER DE SAINT-FARGEAU, 1835: 172. First combination in *Cryptocerus*.

Hypocryptocerus haemorrhoidalis (LATREILLE), WHEELER, 1936 b: 200. First combination in *Hypocryptocerus*.

Zacryptocerus haemorrhoidalis (LATREILLE), BRANDÃO, 1991: 384. First combination in *Zacryptocerus*.

Discussion. - The original description of LATREILLE is too vague on one hand to be useful by present standards, but it contains, on the other hand, some details about the coloration of this species not fitting any of the species presently recognised from Hispaniola. It is easy to suppose, nonetheless, that if the type of this species still exists, its discovery may imply the synonymy of one of the species described in this paper under another name. EMERY (1896) shows that the pigmentation process of callow individuals in *Cephalotes* is not uniform but follows different morphological patterns in different species. On the basis of this observation he suggests that *C. haemorrhoidalis* should be an immature of *C. pusillus*. This guess appears very unlikely (the record of *pusillus* closest to Hispaniola is Trinidad) but the same explanation of incomplete pigmentation may apply much better to any member of the *hamulus* clade. For the time being, any further guess on the true identity of *haemorrhoidalis* would be purely gratuitous.

Distribution: Dominican Republic.

5.8. Keys to the identification of the species

In the following, we present practical keys to the identification of the *Cephalotes* species recognised in this paper. Due to the important morphological differences, three different keys are proposed for the workers, the soldiers and the gynes respectively. A provisional key has been built also for the few known males.

5.8.1. Workers

Workers of *Cephalotes* are easily recognised from soldiers by the dorsally flat pronotum without transverse carina and, in most species, by having protruding eyes not covered by the frontal carinae in dorsal view.

The workers of *klugi* and *prodigiosus* are not included in the key since they are still unknown.

The remaining species can be identified by means of the following key.

1. Vertexal angles bispinose . . . . . (2)
– Vertexal angles differently shaped but never with spines . . . . . (8)
2. Eyes below the antennal scrobes. Vertex without denticles . . . . . (3)
– Eyes behind the antennal scrobes. Vertex with a small pair of denticles . . . (6)
3. Mid and hind basitarsi abruptly narrowing distally in lateral view. Frontal carinae strongly crenulate. Body opaque. Brazil, Peru . . . . . *serraticeps*
– Mid and hind basitarsi not strongly narrowing distally. . . . . (4)
4. CI $\leq$ 122. Frontal carinae not covering completely the genae. Costa Rica, Panama . . . . . *alfaroi*
– CI $\geq$ 127. Frontal carinae covering completely the genae. . . . . (5)
5. Gaster, ventrally, with sparse, pointed hairs. From Costa Rica to Argentina, Belize?, Virgin Islands? . . . . . *atratus*
– Gaster, ventrally, densely covered with pointed hairs. Guyanas, Colombia, Brazil . . . . . *marginatus*

6. Propodeal spines much longer than the basal face of the propodeum. Colombia, Guyana, Brazil, Peru. . . . . *placidus*
– Propodeal spines never as long as the basal face of the propodeum . . . . . (7)
7. CI ≥ 128. PI ≤ 100. Dorsum of the propodeum passing into the lateral faces with a marked ridge. Brazil . . . . . *oculatus*
– CI < 126. PI ≥ 104. Transition between the dorsal and lateral faces of the propodeum simply round. Colombia, Venezuela, Guyanas, Brazil, Ecuador, Peru, Bolivia . . . . . *opacus*
8. Dorsum of the head with long erect hairs . . . . . (9)
– Dorsum of the head with erect hairs either missing or very short . . . . . (25)
9. Basal and declivous faces of the propodeum forming an angle of 90° and separated by a pair of spines. Pronotum with a pair of lateral spines . . . (10)
– Propodeum without distinct basal and declivous faces, i.e., inclined, or, if angulate, the two faces never separate by a pair of spines. Pronotum, laterally, at most denticulate, but never with spines. . . . . (17)
10. Gaster concolour with the body. . . . . (11)
– Gaster coloured differently than the rest of the body . . . . . (14)
11. Posterior fourth of the head dorsum with sparse, thin hairs. Gaster covered with thick, appressed pilosity. Dominican Republic . . . . . *argentiventris*
– Posterior fourth of the head dorsum with curved, thick hairs. Gaster pilosity thinner and much sparser . . . . . (12)
12. Basal face of the propodeum densely covered by appressed, canaliculate hairs hiding the sculpture. Dominican Republic . . . . . *auricomus*
– Basal face of the propodeum with sparse, appressed canaliculate hairs not hiding the sculpture . . . . . (13)
13. Rugosities of the first gastral tergite confined to the articulation area with the postpetiole, otherwise smooth. Dominican Republic (copal) . . . . . *resinae*
– First gastral tergite longitudinally rugose over its entire anterior fourth. At most the gastral lobes can be smooth in some specimens. Dominican Republic, Haiti . . . . . *hamulus*
14. First gastral tergite orange with a black spot in the middle. Dominican Republic, Haiti . . . . . *unimaculatus*
– First gastral tergite orange or reddish-brown but without median spot . . (15)
15. Gaster red. PPeI < 224. Haiti . . . . . *vinosus*
– Gaster orange or brown. PPeI > 235 . . . . . (16)
16. Propodeum almost destitute of pilosity. Gaster orange. Dominican Republic. . . . . *flavigaster*
– Propodeum densely hairy; the pilosity covering the sculpture. Gaster light brown. Dominican Republic (copal). . . . . *taino*
17. First gastral tergite anterolaterally simple, without lobes or expansions . . (18)
– First gastral tergite, anteriorly, bearing a pair of thick lobes or lamella-like expansions. . . . . (22)
18. First gastral tergite with the lateral and posterior borders transparent-yellowish, always much lighter than the rest of the tergite . . . . . (19)
– First gastral tergite with the lateral and posterior borders concolorous with the rest of the tergite . . . . . (20)

19. First gastral tergite bearing, in addition to suberect hairs, a dense covering of long, appressed hairs. Mexico . . . . . *hirsutus*
– Appressed hairs of the first gastral tergite very sparse. Mexico . . . . *insularis*
20. Ventral face of the head with irregular, longitudinal rugosities. Arizona and North Mexico . . . . . *rohweri*
– Ventral face of the head with regular, longitudinal rugosities . . . . . (21)
21. Mesonotum with regular longitudinal rugosities; body superficially shining. Mexico . . . . . *wheeleri*
– Mesonotum with irregular longitudinal rugosities, body opaque. Mexico *toltecus*
22. First gastral tergite anterolaterally with lamellaceous semi-transparent expansions. . . . . (23)
– First gastral tergite anterolaterally with solid lobes . . . . . (24)
23. First gastral tergite with dense, thick, appressed hairs missing only on a pair of longitudinal, posterior stripes. Longitudinal rugulation of the mesosoma superficial. Mexico . . . . . *auriger*
– First gastral tergite with sparse, thick, appressed hairs on the whole surface. Longitudinal rugulation of the mesosoma deeply impressed. Mexico . *chacmul*
24. Erect, truncate hairs sparse (< 50 on the first gastral tergite). Body foveae superficial. Brazil, Paraguay. . . . . *guayaki*
– Erect, truncate hairs dense (> 100 on the first gastral tergite). Body foveae impressed. Brazil, Argentina, Paraguay . . . . . *fiebrigi*
25. Head and mesosoma strongly convex, the convexity very evident also in dorsal view (Fig. 310). Argentina. . . . . *quadratus*
– Head and mesosoma only gently convex or flat . . . . . (26)
26. Body covered with long, pointed, flexuous hairs. . . . . (27)
– Body covering with hairs of different types, but never long, pointed and flexuous. A few pointed hairs may be present on the external border of the frontal carinae and on the sides of the meso- and metasoma, of the petiole, of the postpetiole and on the gaster . . . . . (31)
27. Petiole and postpetiole without lateral spines . . . . . (28)
– Petiole and postpetiole with pronounced lateral spines . . . . . (29)
28. HBaI < 35. Pronotum, laterally, with a pair of projecting, angular expansions (Fig. 246). Dominican amber . . . . . *jansei*
– HBaI ≥ 40. Pronotal lateral expansions much more narrow and obtuse. Dominican amber . . . . . *serratus*
29. Pilosity dense over entire body. Gaster opaque. Cephalic foveae dense and small, i. e. each fovea ~ 1/5 the maximum eye length. Brazil and Paraguay . . . *pilosus*
– Body pilosity sparser. Gaster superficially or completely shining. Cephalic foveae sparse and larger, i. e. each fovea ~ 1/4 the maximum eye length . . (30)
30. Gaster completely shining. Eyes never more than 1/4 of the median head length (mandibles excluded). Argentina . . . . . *liogaster*
– Gaster subopaque. Eyes more than 1/4 of the median head length (mandibles excluded). Argentina. . . . . *lanuginosus*
31. First gastral tergite with massive anterior lobes concolorous with the rest of the gaster. Body colour reddish brown, dark brown or black. Hind Femora never angulate . . . . . (32)
– First gastral tergite without expansions, or with anterior lamellaceous or membranaceous expansions paler than the rest of the gaster. If semimembranaceous lobes are present (*incertus*) then, colour ferruginous or yellowish brown and hind femora angulate . . . . . (37)

32. Sides of the frontal carinae bearing a row of long, pointed hairs. Argentina . . . . . *supercilii*
– Sides of the frontal carinae with clavate or short, subtruncate hairs, but never with long, pointed hairs . . . . . (33)
33. Sides of the frontal carinae, dorsum of the mesosoma, of the pedicel and posterior part of the first gastral tergite with erect, short, subtruncate hairs. Argentina . . . . . *fossithorax*
– Sides of the frontal carinae with subclavate or clavate hairs. Dorsum of the mesosoma and of the pedicel never with erect, short, subtruncate hairs . . (34)
34. Frontal carinae strongly upturned over and behind the eyes, with a clearly upraised external border. Brazil, Argentina . . . . . *bruchi*
– Frontal carinae never upturned above the eyes, only weakly differentiate from the cephalic convexity . . . . . (35)
35. Head, mesosoma, pedicel, gaster and legs only very superficially foveolate; the foveae almost indistinguishable on the first gastral tergite. (Fig. 291). HBaI $\geq$ 30. Argentina and Paraguay . . . . . *bohlsi*
– At least head and mesosoma with deep foveae; foveae of the first gastral tergite always well visible (Figs. 292, 318). HBaI $\leq$ 27. . . . . (36)
36. First gastral sternite shining, the reticulation very superficial. Head, mesosoma and pedicel with impressed sculpture. Foveae on the head and mesosoma dense and deep (Fig. 318). Argentina . . . . . *bivestitus*
– First gastral sternite reticulate and opaque. Head, mesosoma, pedicel and gaster with less impressed sculpture. Foveae on the head and mesosoma sparse and shallow (Fig. 292). Brazil, Argentina, Paraguay . . . . . *jheringi*
37. First gastral tergite completely surrounded by a membranaceous or lamellaceous border . . . . . (38)
– First gastral tergite without expansions or, if a membranaceous or lamellaceous border is present, it never extends to the whole gaster. . . . . (41)
38. Pronotum, laterally, with a pair of broad lamellaceous expansions fused with a spine visible in transparency. Body foveae absent to superficial; hairs simple to broad . . . . . (39)
Pronotum, laterally, with a pair of continuous lamellae not fused with a spine. Body foveae deep, the foveae bearing palm leaf-shaped hairs (Fig. 389). Panama, Peru, Colombia, Bolivia . . . . . *foliaceus*
39. Body shining. Colour yellow. Trinidad & Tobago, from Colombia to Argentina and Paraguay . . . . . *clypeatus*
– Body opaque. Colour darker . . . . . (40)
40. Colour light brown. Membranaceous expansions of the body semitransparent. Brazil . . . . . *membranaceus*
– Colour dark brown to black. Membranaceous expansions of the body whitish. Brazil . . . . . *ustus*
41. Frontal carinae with a deep incision over the eyes . . . . . (42)
– Frontal carinae straight, not incised, over the eyes. . . . . (51)

Note: the following species of the *pallens* clade (dichotomies 42–50) may be difficult to identify when only workers are available. The following part of the key relative to the *pallens* clade should be operational in most instances but we strongly recommend verification of the identifications reached in this way by means of the key to the soldiers whenever possible.

42. Propodeum with a pair of lateral teeth or denticles. Lateral expansions of the petiole truncate and shorter than the maximum length of the petiole. Florida, Bahamas, Cuba . . . . . *varians*
– Propodeum differently shaped, either without denticles or with two or three pairs of denticles. Lateral expansions of the petiole spiniform and as long as or longer than the maximum length of the petiole . . . . . (43)
43. HBaI (Hind Basitarsal Index) ≤ 35 . . . . . (44)
– HBaI (Hind Basitarsal Index) > 38 . . . . . (45)
44. Propodeum, laterally, with two or three pairs of denticles. PPeI < 138. PPpI < 149. Mexico to Ecuador. . . . . *porrasi*
– Propodeum, laterally, without denticles. PPeI > 155. PPpI > 173. Jamaica . . . . . *jamaicensis*
45. Propodeal sides, posteriorly, with one or two pairs of incisions. Mexico to Brazil. . . . . *pallens*
– Propodeal sides without incisions. . . . . (46)
46. Head, mesosoma, pedicel and gaster deeply sculptured; the foveae with thick border, irregular, contiguous and deep (Figs. 215, 218); first gastral tergite with well recognisable sculpture over its whole surface . . . . . (47)
– Head, mesosoma, pedicel and gaster with more superficial sculpture; the foveae with thin border, regular, with narrow interspaces and shallow; the first gastral tergite with very reduced sculpture, nearly smooth on the center . . . . . (48)
47. Border of the frontal carinae strongly crenulate, with several standing, clavate hairs (Fig. 218). Ventral face of the head simply reticulate. Guyana, Surinam, Brazil and Bolivia . . . . . *pallidus*
– Border of the frontal carinae weakly crenulate, only with few clavate hairs (Fig. 215). Ventral face of the head reticulate and with superimposed irregular, longitudinal rugosities. Brazil . . . . . *patellaris*
48. HBaI (Hind Basitarsal Index) < 43 . . . . . (49)
– HBaI (Hind Basitarsal Index) ≥ 50 . . . . . (50)
49. Body superficially shining. Lobes of the first gastral tergite not strongly protruding anteriorly, their maximum length much shorter than their width. Haiti, Dominican Republic . . . . . *decoloratus*
– Body opaque. Lobes of the first gastral tergite strongly protruding anteriorly, their maximum length subequal to the maximum width. Colombia, Venezuela . . . . . *decolor*
50. Anterior border of the frontal carinae with three or four pairs of clubbed hairs. Venezuela, Trinidad, Guyana, Brazil, Bolivia . . . . . *pallidoides*
– Anterior border of the frontal carinae without or at most with one pair of clubbed hairs. Brazil, Bolivia and Paraguay . . . . . *pellans*
51. Antennal club consisting of the last two antennomeres . . . . . (52)
– Antennal club consisting of the last three antennomeres . . . . . (70)
52. Sides of the pronotum generally without denticles and broadly expanded. If the pronotal expansions are weakly denticulate (*kukulcan*, *scutulatus*, *incertus*, *caribicus*) and narrow (*incertus*, *caribicus*, *kukulcan*), the hind femora are angulate . . . . . (53)
– Sides of the pronotum with a narrow, denticulate lamella. If the pronotum is only weakly denticulate (*bimaculatus*), the hind femora are not angulate . (66)
53. Hind femora with a longitudinal crest . . . . . (54)
– Hind femora without a longitudinal crest . . . . . (58)

54. Fore femora with ventral crest. Mexican amber . . . . . *maya*
– Fore femora without ventral crest. . . . . (55)
55. HBaI (Hind Basitarsal Index) = 61.5. Fore femora with a narrow dorsal crest. Mexican amber . . . . . *olmecus*
– HBaI (Hind Basitarsal Index) < 49. Fore femora without dorsal crest . . . (56)
56. Membranaceous expansions of the gaster flat, not bent dorsally neither concave. Costa Rica to Brazil and Bolivia . . . . . *grandinosus*
– Membranaceous expansions of the gaster bent dorsally and concave. . . . (57)
57. Body hairs very broad, almost triangular and appressed, entirely contained in the foveae (Fig. 205). Brazil and Bolivia. . . . . *persimplex*
– Body hairs less broad and simply curved, clearly projecting over the dorsal surface of the head (Fig. 201). Brazil, Argentina and Paraguay . . . . *persimilis*
58. Gaster with semimembranous anterior lobes. Brazil, Argentina, Paraguay. . . . . *incertus*
– Gaster without semimembranous lobes. . . . . (59)
59. Petiole without membranaceous expansions and with a pair of lateral spines. Propodeum laterally incised . . . . . (60)
– Petiole with broad membranaceous lateral expansions, never with true spines. Propodeal sides never incised . . . . . (61)
60. Frontal carinae strongly upturned over the eyes. Vertexal angles with a pair of broad, round expansions. Mexico to Colombia, Venezuela and Ecuador. . . . . *scutulatus*
– Frontal carinae only slightly upturned over the eyes. Vertexal angles with narrow expansions. Mexico, Belize, Costa Rica? . . . . . *kukulcan*
61. Lateral membranaceous expansions of the propodeum straight and narrowing backwards. Dominican amber . . . . . *caribicus*
– Membranaceous expansions of the propodeum convex and broadening medially . . . . . (62)
62. Maximum diameter of the eyes ≥ 0.35 of the median head length. Mexico to Paraguay . . . . . *maculatus*
– Maximum diameter of the eyes ≤ 0.28 of the median head length . . . . . (63)
63. Foveae on the head dorsum very deep and irregular. Membranaceous expansions of the gaster bent dorsally and concave. Brazil . . . . . *liepini*
– Foveae on the head dorsum shallower and more regular. Membranaceous expansions of the gaster flat . . . . . (64)
64. Head (mandibles excluded) longer than the maximum pronotal width. Lower meso- and metapleurae with more than 40 appressed, canaliculate hairs. Argentina . . . . . *pileini*
– Head (mandibles excluded) shorter than the maximum pronotal width. Lower meso- and metapleurae with less than 25 appressed, canaliculate hairs. . . (65)
65. Promesonotal suture impressed. Propodeal suture deeply impressed. Mesosoma with irregular, longitudinal rugosities. Brazil . . . . . *nilpiei*
– Promesonotal suture almost invisible. Propodeal suture visible only as a difference in sculpturation. Longitudinal rugosities of the mesosoma distinguishable only in the propodeal area. Brazil and Paraguay. . . . . *pinelii*
66. Propodeum with only one pair of lateral denticles. Lateral expansions of the petiole and postpetiole shorter than half of the maximum length of the respective segment. Mexico. . . . . *bimaculatus*

– Propodeum with three pairs of lateral denticles. Lateral expansions of the petiole and postpetiole longer than the maximum length of the respective segment . . . . . (67)
67. Hind femora angulate . . . . . (68)
– Hind femora simply curved, without angles or denticles . . . . . (69)
68. Posterior face of the femora with thick, longitudinal rugosities. Ventral part of the first gastral tergite with longitudinal rugosities. Honduras . . . . . *lenca*
– Posterior face of the femora without thick longitudinal rugosities. Ventral part of the first gastral tergite without rugosities. ?Guatemala . . . . . *sobrius*
69. Ventral face of the head with thick, regular, longitudinal striae. Sides of the first gastral sternite with thick, curved striae. Costa Rica . . . . . *curvistriatus*
– Ventral face of the head with thin, irregular, longitudinal rugosities only. Sides of the first gastral sternite with thin, longitudinal rugosities. Texas, North Mexico . . . . . *texanus*
70. Second pair of pronotal teeth in shape of triangular lobes and directed upwards. Hind femora not angulate. Postpetiole with long spines . . . . . (71)
– Pronotum generally without teeth, or, if toothed, the second pair of teeth never lobiform . . . . . (72)
71. Gaster smooth and shining. Peru . . . . . *dentidorsum*
– Gaster punctate and opaque. Brazil . . . . . *adolphi*
72. Fore femora medially incrassate . . . . . (73)
– Fore femora not incrassate . . . . . (82)
73. Colour of the frontal carinae lighter than the rest of the head . . . . . (74)
– Frontal carinae concolour with the head or at least dark ferrugineous brown and infuscate . . . . . (76)
74. First gastral tergite reticulate and with superimposed thin, irregular, longitudinal rugosities. Colombia, Venezuela . . . . . *femoralis*
– First gastral tergite simply reticulate, without rugosities . . . . . (75)
75. Maximum diameter of the eyes more than 1/3 of the head length (mandibles excluded). Pronotal lamellae with three pairs of teeth. Colombia, Guyana, Brazil, Peru . . . . . *manni*
– Maximum diameter of the eyes less than 1/3 of the head length (mandibles excluded). Pronotal lamellae without teeth and anteriorly obtuse. Dominican amber . . . . . *brevispineus*
76. The pair of spines between basal and declivous face of the propodeum longer than the basal face. Peru . . . . . *inca*
– The pair of spines between basal and declivous face of the propodeum shorter than the basal face . . . . . (77)
77. HBaI (Hind Basitarsal Index) > 47 . . . . . (78)
– HBaI (Hind Basitarsal Index) < 43 . . . . . (79)
78. Body more or less shining. Sculpture very superficial. Propodeum with only one pair of spines. Brazil, Peru, Bolivia . . . . . *cordiae*
– Body opaque. Sculpture impressed. Propodeum with two or three pairs of teeth. Colombia, Ecuador, Brazil, Peru, Bolivia . . . . . *ramiphilus*
79. Outer face of the fore femora with longitudinal rugosities. Colombia, Venezuela . . . . . *mompox*
– Outer face of the fore femora without rugosities . . . . . (80)
80. Ventral part of the first gastral tergite shining and with few hairs. Colombia to Brazil, Peru, and Bolivia . . . . . *complanatus*

– Ventral part of the first gastral tergite subopaque and hairy. . . . . (81)
81. Declivous face of the propodeum and ventral part of the first gastral tergite with thin, longitudinal rugosities. Mexico to Ecuador . . . . . *basalis*
– Declivous face of the propodeum and ventral part of the first gastral tergite superficially reticulate and without rugosities. Costa Rica, Panama . . . . . *cordiventris*
82. Maximum diameter of the eyes more than 1/3 of the head length (mandibles excluded) . . . . . (83)
– Maximum diameter of the eyes smaller than 1/3 of the head length (mandibles excluded) . . . . . (84)
83. Second pair of propodeal teeth continuing into the declivous face as a lamella. Colombia, Guyanas, Brazil, Peru, Bolivia . . . . . *simillimus*
– Second pair of propodeal teeth separate from the declivous face. Mexico to Argentina and Paraguay . . . . . *minutus*
84. Cheeks completely without hairs. Colombia and Brazil.. . . . . *duckei*
– Cheeks always more or less hairy . . . . . (85)
85. Pronotum with two pairs of spines or with only one pair of pointed spines followed by denticles (*pusillus*, *columbicus* and *solidus*) but never simply denticulate. . . . . (86)
– Pronotum with a series of denticles or lamellaceous, never spinose . . . . (92)
86. Vertexal angles rounded. Propodeum simply angulate, without teeth or spines. Brazil . . . . . *solidus*
– Vertexal angles truncate. Propodeum with two pairs of spines or with a pair of teeth followed by a pair of spines . . . . . (87)
87. Mesonotum unarmed. Trinidad, Colombia to Brazil and Bolivia . . . *spinosus*
– Mesonotum armed with denticles or teeth . . . . . (88)
88. First gastral tergite with a narrow, semitransparent lamella reaching at most the stigma posteriorly . . . . . (89)
– First gastral tergite with a broad, transparent lamella surpassing the stigma posteriorly . . . . . (91)
89. Spines between the basal and declivous faces of the propodeum at maximum as long as the basal face. Panama, Colombia, Venezuela . . . . . *christopherseni*
– Spines between the basal and declivous faces of the propodeum at least 1.5 times longer than the basal face . . . . . (90)
90. CI $\geq$ 137. PPpI > 226. Foveae on the mesosoma dense. First gastral tergite with deep reticulation. Colombia, Venezuela . . . . . *columbicus*
– CI $\leq$ 133. PPpI < 209. Foveae on the mesosoma sparser. First gastral tergite with superficial reticulation. Colombia to Argentina and Paraguay . . . . . *pusillus*
91. Pilosity dense; on the gaster the space between two hairs subequal to hair thickness. Brazil . . . . . *inaequalis*
– Pilosity sparse; on the gaster the space between two hairs twice or more broader than the hair thickness. Brazil . . . . . *laminatus*
92. Propodeal sides unarmed or armed with 1 to 6 pairs of irregular denticles (93)
– Propodeal sides with a pair of spines followed by a pair of teeth, or simply with lamellaceous or crenulate borders, never denticulate . . . . . (116)
93. Pronotal sides with a narrow, denticulate lamella . . . . . (94)
– Pronotal sides with a broad, rectangular, obtuse or pointed lamella, at most incised in the middle but never denticulate . . . . . (106)

94. Hind femora not angulate . . . . . (95)
– Hind femora angulate. . . . . (102)

Note: *C. conspersus* workers may have angulate and not angulate hind femora. This species has been entered twice into the key under dichotomies 95 and 102.

95. Postpetiolar spines longer than their maximum length. Brazil . . . . . *frigidus*
– Postpetiolar spines shorter than their maximum length . . . . . (96)
96. Ventral face of the head with longitudinal rugosities. Brazil. . . . . *notatus*
– Ventral face of the head reticulate, without longitudinal rugosities. . . . . (97)
97. First gastral sternite almost completely longitudinally striate. Brazil . . . . . *pallidicephalus*
– First gastral sternite reticulate or with striae or rugosities on the sides only (98)
98. First gastral tergite orange to light brown and with a black lozenge in the middle. Body sculpture very superficial. Brazil . . . . . *conspersus* (in part)
– First gastral tergite black with or without a transversal strip or with a pair of variably developed coloured spots. Body sculpture impressed . . . . . (99)
99. Pronotum broader than the head length (mandibles excluded). Gaster completely black. Colombia . . . . . *palta*
– Pronotum as broad as or narrower than the head length. . . . . (100)
100. Petiolar dorsum unarmed. Lateral expansions of the postpetiole round. Postpetiole without dorsal carina. Vertexal angles with broad, transparent lamellae. Brazil . . . . . *goeldii*
– Petiolar dorsum with a minute pair of denticles. Lateral expansions of the postpetiole pointed or obtuse. Postpetiole with traces of a V-shaped carina. Vertexal angles without or simply with narrow lamellae. . . . . (101)
101. Petiole anteriorly oblique. Postpetiole with a well marked V-shaped carina. Margination of the first gastral tergite not surpassing the anterior half of the tergite posteriorly. Venezuela, Trinidad, Guyana, Brazil, Bolivia, Paraguay . . . . . *targionii*
– Petiole anteriorly truncate. Postpetiole with a superficial V-shaped carina. Margination of the first gastral tergite surpassing abundantly the anterior half of the tergite backwards. Brazil and Argentina . . . . . *angustus*
102. Frontal carinae strongly upturned over the eyes. Peru . . . . . *peruviensis*
– Frontal carinae straight or only weakly upturned over the eyes. . . . . (103)
103. First gastral tergite orange to light brown, with a black lozenge in the middle. Brazil . . . . . *conspersus* (in part)
– First gastral tergite black, with or without a pair of anterolateral coloured spots, never with a median lozenge . . . . . (104)
104. PPeI $\leq$ 164. PPpI $\leq$ 151. Brazil, Peru . . . . . *trichophorus*
– PPeI $\geq$ 180. PPpI $\geq$ 160 . . . . . (105)
105. Sides of the first gastral tergite with very fine, longitudinal rugosities. Propodeal suture superficial. Colombia . . . . . *coffeae*
– Sides of the first gastral tergite reticulate. Propodeal suture well marked. Costa Rica, Panama, Colombia . . . . . *setulifer*
106. Gaster extremely globose (Fig. 252). Dominican amber. . . . . *ventriosus*
– Gaster not globose . . . . . (107)
107. Hind femora angulate. . . . . (108)
– Hind femora not angulate . . . . . (112)
108. Propodeum unarmed. Postpetiolar expansions pointed . . . . . (109)
– Propodeum armed. Postpetiolar expansions round . . . . . (110)

109. Body sculpture impressed. CI ≤ 114. Dominican amber . . . . . *dieteri*
– Body sculpture superficial. CI ≥ 120. Dominican amber . . . . . *integerrimus*
110. Body foveae deep and dense, contiguous to each other, their interspaces narrower than the foveae themselves (Fig. 254). Dominican amber . . *obscurus*
– Body foveae more superficial and sparse, their interspace much broader than the maximum fovea diameter (Figs. 253, 258). . . . . (111)
111. First gastral tergite with a dark spot in the middle. Mesosoma with thin, irregular rugosities between the foveae. Dominican amber . . . . . *sucinus*
– First gastral tergite unicolour. Mesosoma without rugosities. Dominican amber . . . . . *bloosi*
112. Gaster with a pair of coloured spots . . . . . (113)
– Gaster without coloured spots . . . . . (114)
113. Gaster anteriorly without crest or lamella. Venezuela, Colombia. . *crenaticeps*
– Gaster anteriorly with a narrow, well visible crest. Ecuador . . . . *ecuadorialis*
114. Gaster anteriorly without crest or lamella. Curaçao . . . . . *emeryi*
– Gaster anteriorly with a narrow, well visible crest. . . . . (115)
115. Gaster with many erect clubbed hairs on its whole surface. Dominican amber . . . . . *alveolatus*
– Gaster with rare erect clubbed hairs only posteriorly. Colombia . . . . . *patei*
116. Dorsum of the mid and hind femora only with sparse, appressed hairs. Petiolar and postpetiolar lateral expansions with strongly crenulate borders. Mexico to Peru and Bolivia . . . . . *umbraculatus*
– Dorsum of the mid and hind femora densely covered with hairs. Petiolar and postpetiolar expansions spiniform or round, never crenulate . . . . . (117)
117. Propodeal sides with a pair of spines followed by a pair of teeth (Figs. 158, 147). . . . . (118)
– Propodeal sides with a lamella, or unarmed, or medially with a broad, triangular lamellaceous expansion but never spinose . . . . . (125)
118. Dorsum of the mesosoma, erect of the pedicel and of the gaster, and legs with abundant erect hairs (Fig. 158). Brazil, Bolivia, Argentina, Paraguay . *eduarduli*
– Mesosoma and pedicel without or with few hairs . . . . . (119)
119. Anterior face of the petiole separated from the lateral ones by an angle . (120)
– Anterior face of the petiole continuing into the lateral ones without marked interruption . . . . . (123)
120. Meso- and metapleurae moderately hairy: at most with 70 hairs . . . . . (121)
– Meso- and metapleurae very hairy, with more than 100 hairs . . . . . (122)
121. Foveae on the head dorsum dense and deep. Posterior third of the propodeum with longitudinal rugosities and few hairs. Brazil. . . . . *betoi*
– Foveae on the head dorsum sparse and shallow. Posterior third of the propodeum superficially reticulate and without hairs. Colombia, Guyanas, Brazil, Peru . . . . . *pavonii*
122. Vertex without denticles. Dorsum of the propodeum largely covered by hairs. Propodeal suture superficial. Venezuela to Bolivia, Argentina, Paraguay . . *depressus*
– Vertex with a pair of small denticles. Dorsum of the propodeum with hairs only on the two anterior thirds. Propodeal suture impressed. Mexico to Colombia . . . . . *cristatus*
123. Frontal carinae almost concolour with the head. Vertexal angles with two pairs of small denticles. Brazil, Argentina and Paraguay. . . . . *borgmeieri*

– Frontal carinae yellow and semitransparent, not concolour with the head. Vertexal angles never denticulate, with a yellowish, lamellaceous border. (124)
124. PI ≤ 97. Guyana, Brazil . . . . . *palustris*
– PI ≥ 103. Colombia, French Guyana, Brazil, Peru, Bolivia. . . . . *cordatus*
125. Vertex with a pair of denticles . . . . . (126)
– Vertex without denticles . . . . . (129)
126. HBaI (Hind Basitarsal Index) > 42. External border of the pronotal lamella continuous. Dominican amber. . . . . *squamosus*
– HBaI (Hind Basitarsal Index) < 32. External border of the pronotal lamella incised . . . . . (127)
127. PpeI ≥ 205. PPpI ≥ 184. Sides of the propodeum with a triangular expansion. Mexico . . . . . *goniodontus*
– PpeI ≤ 200. PPpI ≤ 176. Sides of the propodeum with triangular or obtuse expansion continuing backwards with a lamella . . . . . (128)
128. Body shining. Foveae sparse. Propodeum with reduced, rounded lateral expansions. Mexico to Guatemala . . . . . *biguttatus*
– Body opaque. Foveae denser. Propodeum with projecting triangular expansions. Mexico, Costa Rica and Panama. . . . . *multispinosus*
129. CI = 183. Head and mesosoma greatly flattened and with broad lamellar expansions. Anterior border of the pronotum straight. Mexican amber. . . . *poinari*
– CI = 142. Head and mesosoma of the usual shape. Anterior border of the pronotum curved. Dominican amber . . . . . *hispaniolicus*

5.8.2. Soldiers

Soldiers of *Cephalotes* are easily recognised from workers by the presence of a transverse carina on the pronotum and, often, by having the eyes hidden by the frontal carinae in dorsal view. The pronotal carina appears to be missing only in *manni* (known on a single soldier) but, in this species, the eyes are hidden by the frontal carinae, the head is dorsally convex and the mesosoma is flat and laterally expanded in a typical soldier morphological syndrome.

The following species almost certainly don't have a soldier caste:

argentiventris, *atratus*, *auricomus*, *flavigaster*, *hamulus*, *marginatus*, *oculatus*, *placidus*, *resinae*, *taino*, *unimaculatus*, *vinosus*.

The following species almost certainly do have a soldier caste but it has not yet been described:

adolphi, *auriger*, *dentidorsum*, *ecuadorialis*, *emeryi*, *femoralis*, *hirsutus*, *inca*, *klugi*, *lenca*, *mompox*, *peruviensis*, *solidus*, *trichophorus*, †*alveolatus*, †*bloosi*, †*brevispineus*, †*caribicus*, †*dieteri*, †*hispaniolicus*, †*integerrimus*, †*jansei*, †*maya*, †*obscurus*, †*poinari*, †*serratus*, †*squamosus*, †*sucinus*, †*ventriosus*.

The 41 species listed above, hence, are not considered in the following key.

The soldiers of three species for which soldiers have not been described but in which the gynes are known may be tentatively identified using the key to the gynes. These species are *inca*, *ecuadorialis* and *klugi*.

There are sometimes large and small individuals with the soldier morphology. The following key should apply to both, but, of course, maximum size soldiers are easier to identify.

1. Eyes below the antennal scrobes . . . . . (2)
– Eyes behind the antennal scrobes. . . . . (3)

2. Mid and hind basitarsi, in lateral view, abruptly narrowing distally. Gaster with deep reticulation and opaque. Brazil, Peru . . . . . *serraticeps*
– Mid and hind basitarsi not strongly narrow distally. Gaster with very superficial reticulation and shining. Costa Rica, Panama . . . . . *alfaroi*
3. Anterolateral border of the first gastral tergite bearing a lamella bent ventrally. Gaster strongly convex dorsally. Propodeum with a pair of spines. Colombia, Venezuela, Guyanas, Brazil, Ecuador, Peru, Bolivia . . . . . *opacus*
– Anterolateral border of the first gastral tergite bearing a straight lamella, never bent ventrally. Gaster not strongly convex dorsally. . . . . (4)
4. Mandibles simply convex, without tumuli or denticles . . . . . (5)
– Mandibles with a lateral tumulus or with an obtuse, carinate denticle . . . (12)
5. CI < 108. Frontal carinae converging over the eyes. Vertex, medially, with a transverse carina . . . . . (6)
– CI > 113. Frontal carinae straight over the eyes. Vertex at least with traces of a pair of denticles . . . . . (7)
6. Declivous face of the propodeum with longitudinal rugosities. Pronotal carina well developed. Mexico to Argentina and Paraguay . . . . . *minutus*
– Declivous face of the propodeum simply reticulate, never rugose. Pronotal carina superficial. Colombia, Guyanas, Brazil, Peru, Bolivia. . . . . *simillimus*
7. Anterolateral gastral lamellae broad, protruding and transparent. PPeI ≤ 254 (8)
– Anterolateral gastral lamellae narrow and semitransparent. PPeI ≥ 260 . . (10)
8. Frontal carinae orange and transparent. Pronotal sides with two pairs of pointed spines. Trinidad and Colombia to Brazil and Bolivia . . . . . *spinosus*
– Frontal carinae dark ferrugineous, semitrasparent or infuscate. Pronotal sides with two pairs of teeth, the first triangular and the second obtuse. . . . . (9)
9. Sides of the frontal carinae gently converging anteriorly, not forming an angle. Body subopaque. Brazil. . . . . *inaequalis*
– Sides of the frontal carinae strongly converging anteriorly and angulate. Body shining. Brazil . . . . . *laminatus*
10. Vertex with a pair of salient denticles. Body sculpture superficial. Panama, Colombia, Venezuela. . . . . *christopherseni*
– Vertex only with traces of denticles. Body sculpture impressed . . . . . (11)
11. PPeI ≥ 305. PPpI ≥ 276. Foveae impressed. Colombia, Venezuela . *columbicus*
– PPeI ≤ 290. PPpI ≤ 233. Foveae superficial. Colombia to Argentina and Paraguay. . . . . *pusillus*
12. Cheeks completely without hairs. Cephalic disc incomplete. Colombia, Brazil . . . . . *duckei*
– Cheeks always more or less hairy. Cephalic disc usually (not in all species) complete. . . . . (13)
13. Fore femora medially incrassate. Propodeal sides "plate-like" . . . . . (14)
– Fore femora not incrassate. Propodeal sides round, angulate or denticulate (19)
14. Frontal carinae crenulate and with clubbed hairs. Mesosoma flat. Pronotal crest absent. Colombia, Guyana, Brazil, Peru . . . . . *manni*
– Frontal carinae straight and hairless. Mesosoma convex. Pronotal crest superficial to well marked . . . . . (15)
15. Vertex with a pair of denticles. First gastral tergite anterolaterally with a pair of tufts of silvery hairs . . . . . (16)
– Vertex without denticles. First gastral tergite anterolaterally without tufts of hairs . . . . . (17)

16. CI ≥ 119. HBaI (Hind Basitarsal Index) ≥ 40. Posterior third of the first gastral tergite covered by dense, thick hairs. Mexico to Ecuador . . . . . *basalis*
– CI ≤ 115. HBaI (Hind Basitarsal Index) ≤ 37.5. Posterior third of the first gastral tergite covered by sparse, thin hairs. Costa Rica, Panama . *cordiventris*
17. HBaI (Hind Basitarsal Index) ≤ 45. Pronotal crest strongly marked. Border of the frontal carinae upturned. Colombia to Brazil, Peru and Bolivia . . . . . *complanatus*
– HBaI (Hind Basitarsal Index) > 51. Pronotal crest superficial. Border of the frontal carinae straight, not upturned . . . . . (18)
18. Body sculpture very superficial. Sides of the basal face of the propodeum diverging backwards and ending in a long, pointed spine. Brazil, Peru, Bolivia . . . . . *cordiae*
– Body sculpture impressed. Sides of the basal face of the propodeum convex and ending in a short, triangular tooth. Colombia, Ecuador, Brazil, Peru, Bolivia . . . . . *ramiphilus*
19. Gaster surrounded by a lamella or by an infuscate to transparent lateral expansion . . . . . (20)
– Gaster not surrounded by a lamella or an expansion . . . . . (23)
20. Cephalic disc complete, i. e. well visible over the whole dorsal surface of the head. Antennal club two jointed. Panama, Peru, Colombia, Bolivia . . *foliaceus*
– Cephalic disc incomplete (i. e. recognisable as a round border on the posterior half of the head only) or absent. Antennal club three jointed . . . . . (21)
21. Cephalic disc incomplete but well visible posteriorly. Body light brown. Brazil. . . . . *membranaceus*
– Cephalic disc absent. Colour yellow or black . . . . . (22)
22. Body shining. Colour yellow. Trinidad & Tobago, from Colombia to Argentina and Paraguay . . . . . *clypeatus*
– Body opaque. Colour black. Brazil . . . . . *ustus*
23. Basal and declivous faces of the propodeum continuous, or, if differentiated, the basal face very short, much shorter than the declivous face . . . . . (24)
– Basal and declivous faces of the propodeum well differentiated and separated by an angle. Basal face long, at least subequal to or longer than the declivous face . . . . . (34)
24. Propodeal sides with a lamella or with a triangular, broad lamellaceous tooth. . . . . (25)
– Propodeal sides without lamellae and with a rectangular expansion followed or not by a pointed tooth . . . . . (27)
25. Cephalic disc absent, the head dorsum simply convex. Sculpture shining. Mexico to Guatemala . . . . . *biguttatus*
– Cephalic disc incomplete, recognisable as a round margin on the posterior half of the head only. Sculpture opaque . . . . . (26)
26. Body with dense, impressed foveae. Sides of the propodeum, medially, with a pair of broad, triangular, lamellaceous teeth. Mexico . . . . . *goniodontus*
– Body with sparse, superficial foveae. Propodeum with a pair of lamellae, toothed anteriorly and narrowing backwards. Mexico, Costa Rica and Panama . . . . . *multispinosus*
27. Cephalic disc incomplete, visible only as a round margin on the posterior part of the head . . . . . (28)

– Cephalic disc complete, occupying the whole cephalic dorsum. . . . . (31)
28. Sides of the pronotum, anteriorly, with a pair of pointed, triangular expansions. Meso-and metapleurae with less than 120 canaliculate hairs. Brazil . . . . *betoi*
– Sides of the pronotum with a pair of subtruncate or truncate expansions. Meso- and metapleurae with more than 140 canaliculate hairs . . . . . (29)
29. HBaI (Hind Basitarsal Index) > 43. PPeI ≤ 163. Brazil, Argentina and Paraguay . . . . . *borgmeieri*
– HBaI (Hind Basitarsal Index) ≤ 38. PPeI ≥ 173 . . . . . (30)
30. First gastral tergite without erect hairs. Venezuela to Bolivia, Argentina and Paraguay. . . . . *depressus*
– First gastral tergite with at least 120 erect subclavate hairs. Brazil, Bolivia, Argentina, Paraguay . . . . . *eduarduli*
31. Sides of the pronotum with a broad, rectangular expansion. Mexico to Colombia. . . . . *cristatus*
– Sides of the pronotum with a subtruncate, or subpointed or convex expansion. . . . . (32)
32. Meso- and metapleurae with less than 70 appressed, canaliculate hairs. Colombia, Guyanas, Brazil, Peru . . . . . *pavonii*
– Meso- and metapleurae with more than 100 appressed, canaliculate hairs . (33)
33. HBaI (Hind Basitarsal Index) ≤ 41. Pronotal sides subtruncate. Guyana, Brazil . . . . . *palustris*
– HBaI (Hind Basitarsal Index) > 43. Pronotal sides triangular and subpointed or convex. Colombia, French Guyana, Brazil, Peru, Bolivia . . . . . *cordatus*
34. Pronotal sides with a pair of broad, triangular expansions directed laterally. First gastral tergite yellow and with a brown cross-shaped macula medially, the transversal strip darker than the longitudinal one. Mexico to Peru and Bolivia . . . . . *umbraculatus*
– Pronotal sides never with a broad triangular expansion. Gaster either unicolour or with one or two pairs of coloured spots . . . . . (35)
35. Antennal club consisting of the last two antennomeres . . . . . (36)
– Antennal club consisting of the last three antennomeres . . . . . (66)
36. Cephalic disc, in dorsal view, covering the mandibles . . . . . (37)
– Cephalic disc, in dorsal view, not covering the mandibles. . . . . (46)
37. Foveae of the floor of the cephalic disc contiguous . . . . . (38)
– Foveae of the floor of the cephalic disc separate by interspaces. . . . . (41)
38. Center of the disc with a protruding tumulus. Foveae on the disc contiguous and irregular. Body with impressed sculpture. Guyana, Surinam, Brazil and Bolivia. . . . . *pallidus*
– Center of the disc flat or with a superficial tumulus. Foveae on the disc more regular. Body with superficial sculpture . . . . . (39)
39. HBaI > 50. Hind femora with a marked carina. Venezuela, Trinidad, Guyana, Brazil, Bolivia . . . . . *pallidoides*
– HBaI < 41. Hind femora without carina . . . . . (40)
40. CI = 103. Jamaica. . . . . *jamaicensis*
– CI < 97. Florida, Bahamas, Cuba . . . . . *varians*
41. Foveal hairs of the floor of the disc suberect or, at most, subdecumbent. . (41)
– Foveal hairs of the floor of the disc decumbent to appressed . . . . . (43)
42. Foveal hairs of the cephalic disc brush-shaped. PPeI < 210. PPpI < 210. Mexico to Ecuador . . . . . *porrasi*

– Foveal hairs of the cephalic disc subclavate. PPeI > 216. PPpI > 224. Brazil . . . . . *patellaris*

43. CI > 101. Vertexal angles separate from the disc by a strong impression (Fig. 242). Colombia and Venezuela. . . . . *decolor*

– CI < 96. Vertexal angles without or with only a superficial impression . . (44)

44. Antennal scrobes, posteriorly, ending in front of the eyes. Mexico to Brazil . . . . . *pallens*

– Antennal scrobes, posteriorly, ending below the eyes . . . . . (45)

45. CI ≥ 92. Postpetiolar expansions narrow. Haiti, Dominican Republic. . . . . *decoloratus*

– CI < 88. Postpetiolar expansions broad. Brazil, Bolivia, Paraguay . . . *pellans*

46. Sides of the declivous face of the propodeum at least with a narrow lamella or with a membranaceous expansion. . . . . (47)

– Sides of the declivous face of the propodeum simply marginate . . . . . (58)

47. Hind femora with a crest. . . . . (48)

– Hind femora without a crest . . . . . (51)

48. HBaI (Hind Basitarsal Index) > 66. Mexican amber. . . . . *olmecus*

– HBaI (Hind Basitarsal Index) < 50 . . . . . (49)

49. Floor of the cephalic disc with contiguous, irregular foveae. Costa Rica to Brazil and Bolivia . . . . . *grandinosus*

– Floor of the cephalic disc with foveae separated by interspaces. . . . . (50)

50. Body hairs very broad, almost triangular, appressed, entirely contained in the foveae. Frontal carinae not crenulate; hairs on the frontal carinae rare to absent. Brazil and Bolivia . . . . . *persimplex*

– Body hairs narrower and simply curved, clearly projecting outside the foveae. Frontal carinae superficially to strongly crenulate and with hairs. Brazil, Argentina and Paraguay . . . . . *persimilis*

51. Foveae of the cephalic disc separate by interspaces. Vertex continuous . . (52)

– Foveae of the cephalic disc contiguous. Vertex with a more or less deep depression. . . . . (53)

52. Petiolar and postpetiolar lateral expansions pointed. Mexico to Colombia, Venezuela and Ecuador . . . . . *scutulatus*

– Petiolar and postpetiolar lateral expansions round. Brazil, Argentina, Paraguay . . . . . *incertus*

53. Foveal hairs of the cephalic disc erect or subdecumbent and largely surpassing the foveal border . . . . . (54)

– Foveal hairs of the cephalic disc decumbent or appressed and not surpassing the foveal border . . . . . (56)

54. Petiolar and postpetiolar lateral expansions pointed. Mexico, Belize, ?Costa Rica . . . . . *kukulcan*

– Petiolar and postpetiolar lateral expansions round or obtuse . . . . . (55)

55. Vertex with a very deep median depression. Propodeum with a small pair of short teeth gently directed upwards. Brazil and Paraguay . . . . . *pinelii*

– Vertex with a very superficial median depression. Propodeum without teeth. Brazil . . . . . *liepini*

56. Sides of the pronotum concolour with the rest of the mesosoma. Distal and anterior part of the frontal carinae with a single row of long, appressed hairs (Fig. 384 B). Mexico to Paraguay. . . . . *maculatus*

– Sides of the pronotum with a yellow macula. Distal and anterior part of the frontal carinae with two rows of short, appressed hairs (Figs. 170, 172) . . (57)
57. Propodeum with a pair of short teeth gently directed upwards. PPeI ≥ 222. PPpI ≥ 218. Brazil . . . . . *nilpiei*
– Propodeum without teeth. PPeI ≤ 203. PPpI ≤ 197. Argentina . . . . . *pileini*
58. Foveae of the cephalic disc contiguous . . . . . (59)
– Foveae of the cephalic disc with visible interspaces . . . . . (61)
59. Head and first gastral tergite unicolour. Propodeum with a pair of pointed spines. Arizona and North Mexico . . . . . *rohweri*
– Head bicolour. First gastral tergite with a pair of coloured anterolateral spots. Propodeum without spines . . . . . (60)
60. First gastral tergite entirely covered by irregular, longitudinal rugosities. CI < 106. PPpI > 238. Mexico . . . . . *bimaculatus*
– First gastral tergite reticulate and with rugosities only on the anterior third. CI > 110. PPpI < 217. Texas, North Mexico . . . . . *texanus*
61. Borders of the cephalic disc without hairs . . . . . (62)
– Borders of the cephalic disc hairy . . . . . (64)
62. Floor of the cephalic disc continuously declivous and with a protruding median tumulus. Mexico . . . . . *insularis*
– Floor of the cephalic disc flat posteriorly and oblique anteriorly, with or without a reduced tumulus . . . . . (63)
63. Body sculpture very superficial. Oblique part of the cephalic disc without tumulus. Mexico . . . . . *wheeleri*
– Body sculpture impressed. Oblique part of the cephalic disc with a small tumulus. Mexico . . . . . *toltecus*
64. Frontal carinae yellow-orange. Foveal hairs on the head dorsum thick. Costa Rica. . . . . *curvistriatus*
– Frontal carinae reddish-brown. Foveal hairs of the head dorsum thin . . . (65)
65. PPpI < 192. TL 5.72–6.44. Cephalic disc opaque. Hind femora weakly angulate. ?Guatemala . . . . . *sobrius*
– PPpI ≥ 200.0. TL 4.98–5.32. Cephalic disc shining. Hind femora angulate. Mexico . . . . . *chacmul*
66. Cephalic disc, in dorsal view, covering the mandibles. Costa Rica, Panama, Colombia . . . . . *setulifer*
– Cephalic disc, in dorsal view, not covering the mandibles. . . . . (67)
67. Hind femora angulate. Cephalic disc deeply concave. Basal face of the propodeum with 2–3 pairs of irregular teeth. Colombia . . . . . *coffeae*
– Hind femora not angulate or, if with traces of an angle (*conspersus*), the cephalic disc is flat. Basal face of the propodeum without 2–3 pairs of irregular teeth. . . . . (68)
68. Anterior third of the first gastral tergite densely covered by hairs . . . . . (69)
– Anterior third of the first gastral tergite with sparse hairs. . . . . (70)
69. First gastral tergite with a pair of coloured spots. PPeI ≤ 290. PPpI ≤ 252. HBaI (Hind Basitarsal Index) < 30. Venezuela, Colombia . . . . . *crenaticeps*
– First gastral tergite without spots. PPeI ≥ 300. PPpI ≥ 285. HBaI (Hind Basitarsal Index) = 36. Colombia. . . . . *patei*
70. Cephalic disc incomplete, visible as a round margin on the posterior part of the head only. Brazil, Argentina . . . . . *bruchi*

– Cephalic disc complete, occupying the entire head dorsum . . . . . (71)
71. Body entirely covered by long, flexuous hairs . . . . . (72)
– Body without long flexuous hairs or, if some flexuous hairs are present (*supercilii*), they are restricted to the sides of the head . . . . . (74)
72. First gastral tergite with superficial reticulation and shining, very shining at least on the last third. Argentina . . . . . *liogaster*
– First gastral tergite with impressed reticulation and opaque to subopaque (73)
73. Sides of the mesonotum with small, round expansions. Anterior face of the petiole deeply concave. Argentina . . . . . *lanuginosus*
– Sides of the mesonotum with broad, round expansions. Anterior face of the petiole only gently concave. Brazil, Paraguay, ?Argentina . . . . . *pilosus*
74. Sides of the head with long, flexuous hairs. Head dorsum with two types of hairs: canaliculate and truncate. Argentina . . . . . *supercilii*
– Hairs on the sides of the head clavate or truncate. Head dorsum with only one type of hairs . . . . . (75)
75. Sides of the frontal carinae with subtruncate, short hairs. Sides of the mesosoma and of the pedicel with very short truncate hairs. Argentina . . . . *fossithorax*
– Sides of the frontal carinae with subclavate or clavate hairs. Sides of the mesosoma and of the pedicel with subclavate hairs or hairless . . . . . (76)
76. Foveae of the cephalic disc sparse, with broad interspaces . . . . . (77)
– Foveae of the cephalic disc contiguous . . . . . (80)
77. CI > 105. Pronotum with broad lateral expansions. Brazil and Argentina . . . . . *angustus*
– CI ≤ 100. Pronotum almost straight . . . . . (78)
78. Hind femora gently angulate. PPeI < 208. PPpI < 197. Brazil . . . . *conspersus*
– Hind femora not angulate. PPeI ≥ 230. PPpI ≥ 224 . . . . . (79)
79. Cephalic disc flat. PPeI > 268. PPpI > 244. Colombia . . . . . *palta*
– Cephalic disc convex. PPeI = 230. PPpI = 224. Argentina, Paraguay. . . *bohlsi*
80. Cephalic disc flat or convex . . . . . (81)
– Cephalic disc concave . . . . . (84)
81. PPeI > 240. PPpI > 225. HBaI (Hind Basitarsal Index) > 32. Brazil, Argentina, Paraguay . . . . . *jheringi*
– PPeI < 206. PPpI < 203. HBaI (Hind Basitarsal Index) < 30 . . . . . (82)
82. PPeI > 202. Dorsum of the mesosoma with more than 40 subtruncate, suberect hairs. Brazil, Argentina, Paraguay . . . . . *fiebrigi*
– PPeI < 195. Dorsum of the mesosoma hairless or, at most, with less than 20 subtruncate hairs . . . . . (83)
83. CI = 100. HBaI (Hind Basitarsal Index) = 25.6. Mesosoma with canaliculate hairs. Argentina . . . . . *quadratus*
– CI < 94. HBaI (Hind Basitarsal Index) > 29. Mesosoma with subtruncate hairs mixed with the canaliculate ones. Brazil, Paraguay . . . . . *guayaki*
84. CI > 114. PPeI > 314. PPpI > 286. Pronotum broader than the head width. Brazil . . . . . *goeldii*
– CI < 108. PPeI < 283. PPpI < 247. Pronotum narrower than the head width or at most as broad as the head width . . . . . (85)
85. TL > 10 mm. Antennal scrobes without dorsal carina. Argentina. . . . . *prodigiosus*
– TL < 7.5 mm. Antennal scrobes, dorsally, with a longitudinal carina bearing a denticle . . . . . (86)

86. Posterior fifth of the head disc flat. Remaining part of the disc concave. Argentina . . . . . *bivestitus*
– Head disc entirely concave. . . . . (87)
87. PPeI ≥ 240. PPpI ≥ 221. . . . . (88)
– PPeI < 221. PPpI ≤ 215. . . . . (89)
88. Vertexal angles with broad, lamellaceous borders. Pronotum with broad, lateral expansions. First gastral sternite without or with only superficial, longitudinal rugosities. Brazil . . . . . *notatus*
– Vertexal angles with narrow lamellaceous borders or simply marginate. Pronotum with narrow lateral expansions. First gastral sternite with deep, longitudinal rugosities. Brazil . . . . . *pallidicephalus*
89. Foveae of the cephalic disc very irregular in shape. Vertexal angles with lamellaceous borders. Brazil. . . . . *frigidus*
– Foveae of the cephalic disc round. Vertexal angles simply marginate. Venezuela, Trinidad, Guyana, Brazil, Bolivia, Paraguay . . . . . *targionii*

5.8.3. Gynes

The gynes of the following 50 species are not considered in the key since they are still unknown:

adolphi, *alfaroi*, *argentiventris*, *auriger*, *bohlsi*, *chacmul*, *conspersus*, *dentidorsum*, *emeryi*, *femoralis*, *flavigaster*, *foliaceus*, *goniodontus*, *hirsutus*, *jamaicensis*, *lenca*, *liepini*, *manni*, *mompox*, *nilpiei*, *palta*, *palustris*, *peruviensis*, *quadratus*, *resinae*, *simillimus*, *solidus*, *taino*, *toltecus*, *trichophorus*, *unimaculatus*, *ustus*, *vinosus*, *wheeleri*, †*alveolatus*, †*bloosi*, †*brevispineus*, †*caribicus*, †*dieteri*, †*hispaniolicus*, †*integerrimus*, †*jansei*, †*maya*, †*obscurus*, †*olmecus*, †*poinari*, †*serratus*, †*squamosus*, †*sucinus*, †*ventriosus*.

The gynes of 19 species for which gynes have not yet been described but in which the soldiers are known may be tentatively identified using the key to the soldiers. These species are *alfaroi*, *bohlsi*, *chacmul*, *conspersus*, *dentidorsum*, *foliaceus*, *goniodontus*, *jamaicensis*, *liepini*, *manni*, *nilpiei*, *palta*, *palustris*, *quadratus*, *simillimus*, *toltecus*, *ustus*, *wheeleri*, †*olmecus*.

In *Cephalotes* there are often microgynes. The key is based essentially on wholly developed gynes but it should apply reasonably well to both size classes.

1. Eyes below the antennal scrobes . . . . . (2)
– Eyes behind the antennal scrobes. . . . . (4)
2. Mid and hind basitarsi, in lateral view, abruptly narrowing distally. Brazil, Peru . . . . . *serraticeps*
– Mid and hind basitarsi not strongly narrowing distally. . . . . (3)
3. First gastral sternite densely covered by hairs. Guyanas, Colombia, Brazil . . . . . *marginatus*
– First gastral sternite with sparse hairs. From Costa Rica to Argentina, ?Belize, ?Virgin Islands. . . . . *atratus*
4. Ventral face of the head covered by striae . . . . . (5)
– Ventral face of the head simply reticulate, sometimes foveate or superficially rugose, but never striate . . . . . (6)
5. Basal face of the propodeum entirely and densely covered by hairs. PPeI > 297. Dominican Republic . . . . . *auricomus*
– Only the center of the basal face of the propodeum covered with hairs. PPeI < 274. Dominican Republic, Haiti . . . . . *hamulus*
6. Border of the frontal carinae with a denticle (Fig. 55). . . . . (7)

– Border of the frontal carinae without denticles . . . . . (9)
7. PPpI = 300. Frontal carinae crenulate. Colombia, Venezuela, Guyanas, Brazil, Ecuador, Peru, Bolivia. . . . . *opacus*
– PPpI < 292. Frontal carinae without crenulations or only weakly crenulate (8)
8. PPeI = 312. PPpI = 269. HBaI (Hind Basitarsal Index) < 21. Propodeal spines shorter than the basal face of the propodeum. Brazil . . . . . *oculatus*
– PPeI ≥ 320. PPpI > 281. HBaI (Hind Basitarsal Index) > 25. Propodeal spines at least 1.5 longer than the basal face of the propodeum. Colombia, Guyana, Brazil, Peru . . . . . *placidus*
9. Mandibles simply convex, without lateral tumuli or denticles . . . . . (10)
– Mandibles with a lateral tumulus or with an obtuse, carinate denticle . . . (16)
10. First gastral tergite with two pairs of well visible yellow-orange spots. . . (11)
– First gastral tergite, as a rule, without spots or, if with two pairs of spots, these are reddish and less visible . . . . . (14)
11. TL < 10 mm. Body opaque. In some specimens the gastral spots connected longitudinally. Mexico to Argentina and Paraguay . . . . . *minutus*
– TL > 11.5 mm. Body shining. Gastral spots never connected each other . (12)
12. CI < 111. Pronotal carina well marked. Brazil. . . . . *laminatus*
– CI > 121. Pronotal carina marked only medially or absent . . . . . (13)
13. Frontal carinae semitrasparent. Postpetiolar expansions half so broad as the length of the postpetiole. Trinidad and Colombia to Brazil and Bolivia.*spinosus*
– Frontal carinae nearly concolour with the rest of the head. Postpetiolar expansions slightly more than 1/3 of the postpetiolar length. Brazil . *inaequalis*
14. Head dorsum with very superficial foveae (Fig. 87). First gastral tergite moderately shining and, in most specimens, with two pairs of reddish maculae. Propodeal spines projecting laterally almost at right angle. Panama, Colombia, Venezuela . . . . . *christopherseni*
– Head dorsum with impressed foveae (Fig. 64). First gastral tergite opaque and sometimes with two pairs of ferrugineous maculae. Propodeal spines directed backwards or only slightly diverging . . . . . (15)
15. PPeI > 260. Frontal carinae broad and only weakly converging anteriorly. Colombia, Venezuela. . . . . *columbicus*
– PPeI < 249. Frontal carinae narrow and clearly converging anteriorly. Colombia to Argentina, Paraguay. . . . . *pusillus*
16. Fore femora medially incrassate. . . . . (17)
– Fore femora not incrassate. . . . . (22)
17. First gastral tergite with a pair of yellow-orange spots . . . . . (18)
– First gastral tergite without spots . . . . . (20)
18. Vertex with prominent denticles. Posterior fourth of the first gastral tergite covered by hairs. Mexico to Ecuador . . . . . *basalis*
– Vertex without or only with traces of denticles. Posterior fourth of the first gastral tergite only with a few hairs . . . . . (19)
19. PPpI < 179. HBaI (Hind Basitarsal Index) > 39. First gastral tergite with a pair of orange anterolateral spots. Colombia to Brazil, Peru and Bolivia . . . . . *complanatus*
– PPpI > 187. HBaI (Hind Basitarsal Index) ≤ 37. First gastral tergite with a pair of whitish-yellow spots in the middle of its sides. Costa Rica, Panama . . . . . *cordiventris*

20. Anterior fifth of the first gastral tergite covered with thick, appressed hairs. Peru. . . . . *inca*
– Anterior fifth of the first gastral tergite with sparse hairs . . . . . (21)
21. Body with superficial sculpture and shining. HBaI > 57. PPeI < 168. Brazil, Peru and Bolivia . . . . . *cordiae*
– Body with deep sculpture and opaque. HBaI < 46. PPeI > 178. Colombia, Ecuador and Brazil, Peru, Bolivia . . . . . *ramiphilus*
22. Cephalic disc absent, i. e. the head dorsum normally round . . . . . (23)
– Cephalic disc incomplete, i. e. recognisable on the posterior part of the head only, or complete, occupying the whole head dorsum but always visible . (28)
23. First gastral tergite with two pairs of whitish spots. Colour yellow. Trinidad & Tobago, from Colombia to Argentina and Paraguay. . . . . *clypeatus*
– First gastral tergite either without or only with one pair of spots . . . . . (24)
24. First gastral tergite anterolaterally with one pair of yellow spots. Mexico to Guatemala . . . . . *biguttatus*
– First gastral tergite anterolaterally without spots . . . . . (25)
25. Postpetiole with at least 20 suberect hairs. Brazil, Bolivia, Argentina, Paraguay . . . . . *eduarduli*
– Postpetiole with less than 10 suberect hairs . . . . . (26)
26. CI > 117. PPpI > 207. HBaI (Hind Basitarsal Index) > 41. Colour reddish to dark brown. Brazil, Argentina and Paraguay. . . . . *borgmeieri*
– CI < 114. PPpI < 197. HBaI (Hind Basitarsal Index) < 39. Colour black . (27)
27. PPeI > 226. Lower metapleurae with at least 30 appressed hairs. Frontal carinae semitrasparent. Venezuela to Bolivia, Argentina and Paraguay . . . . *depressus*
– PPeI < 213. Lower metapleurae with at most 15 appressed hairs. Frontal carinae infuscate . . . . . *betoi*
28. Cephalic disc incomplete, visible as a round margin on the posterior part of the head only . . . . . (29)
– Cephalic disc complete, covering the head dorsum . . . . . (35)
29. Cheeks without appressed hairs. Colombia and Brazil. . . . . *duckei*
– Cheeks with appressed hairs. . . . . (30)
30. First gastral tergite, anterolaterally, with a pair of yellow spots. Sides of the propodeum gently convex and with irregular border. Mexico, Costa Rica and Panama . . . . . *multispinosus*
– First gastral tergite either without or with two pairs of spots. Sides of the propodeum armed with teeth or spines. . . . . (31)
31. Colour light brown. First gastral tergite with two pairs of yellowish spots. Brazil . . . . . *membranaceus*
– Colour black. First gastral tergite without spots. . . . . (32)
32. Propodeum with a pair of spines. Vertex with or without traces of minute denticles. Brazil and Argentina . . . . . *bruchi*
– Propodeum with two pairs of teeth. Vertex with prominent denticles . . . (33)
33. PPeI < 189. PPpI < 155. HBaI (Hind Basitarsal Index) > 46. Colombia, French Guyana, Brazil, Peru, Bolivia. . . . . *cordatus*
– PPei > 226. PPpI > 179. HBaI (Hind Basitarsal Index) < 37 . . . . . (34)
34. Lower metapleurae with more than 15 appressed hairs. Mexico to Colombia . . . . . *cristatus*
– Lower metapleurae with at most 5 appressed hairs. Colombia, Guyanas, Brazil, Peru . . . . . *pavonii*

35. Frontal carinae, in dorsal view, covering the mandibles . . . . . (36)
– Frontal carinae not covering the mandibles in dorsal view . . . . . (45)
36. First gastral tergite with a pair of orange spots. Costa Rica, Panama, Colombia . . . . . *setulifer*
– First gastral tergite without spots . . . . . (37)
37. Foveal hairs of the cephalic disc brush-shaped. Mexico to Ecuador. . . *porrasi*
– Foveal hairs of the cephalic disc subclavate. . . . . (38)
38. Foveal hairs of the floor of the disc erect or suberect . . . . . (39)
– Foveal hairs of the floor of the disc subdecumbent or appressed . . . . . (41)
39. Cephalic disc with a protruding medial tumulus. HBaI (Hind Basitarsal Index) ≤ 45 . . . . . (40)
– Cephalic disc at most gently convex medially, without tumulus. HBaI (Hind Basitarsal Index) ≥ 50. Venezuela, Trinidad, Guyana, Brazil, Bolivia . . . . . *pallidoides*
40. Foveae of the floor of the disc irregular and contiguous. Guyana, Surinam, Brazil and Bolivia . . . . . *pallidus*
– Foveae of the floor of the disc regular and sparse. Brazil . . . . . *patellaris*
41. PPpI > 231. Postpetiolar expansions absent or very reduced. Florida, Bahamas, Cuba. . . . . *varians*
– PPpI < 218. Postpetiolar expansions always well developed . . . . . (42)
42. PPeI > 234. . . . . (43)
– PPeI < 230. . . . . (44)
43. Posterior border of the disc strongly crenulate. Pronotal crest well marked. Mexico to Brazil. . . . . *pallens*
– Posterior border of the disc weakly crenulate. Pronotal crest superficial. Brazil, Bolivia and Paraguay . . . . . *pellans*
44. CI < 89. TL < 8.5 mm. Hispaniola . . . . . *decoloratus*
– CI $\geq$ 96. TL $\geq$ 9.8 mm. Colombia, Venezuela. . . . . *decolor*
45. First gastral tergite yellow to light brown with a pair of dark brown spots, sometimes the spots connected each other and a third, median superficial, thin, longitudinal strip may be also present . . . . . (46)
– First gastral tergite black, either without, or with one, or two pairs of yellow spots; if the tergite is light brown with two pairs of spots, these are yellowish . . . . . (50)
46. TL > 11 mm. PPeI $\geq$ 260. Mexico to Peru and Bolivia . . . . . *umbraculatus*
– TL < 8.4 mm. PPeI < 247 . . . . . (47)
47. Foveae on the floor of the disc irregular. Costa Rica, Panama, Colombia, Venezuela, Trinidad, Guyana, Brazil, Bolivia . . . . . *grandinosus*
– Foveae on the floor of the disc regular . . . . . (48)
48. CI = 114. PPeI > 246. Whole border of the frontal carinae transparent, upturned and high. Brazil . . . . . *klugi*
– CI $\leq$ 106. PPeI $\leq$ 232. Border of the frontal carinae concolour with the rest of the head, upturned and slightly high only anteriorly . . . . . (49)
49. Frontal carinae crenulate. Body hairs very broad, almost triangular, appressed, entirely contained in the foveae. Brazil, Argentina and Paraguay. . . *persimilis*
– Frontal carinae weakly crenulate. Body hairs narrower and simply curved, clearly projecting outside the foveae. Brazil and Bolivia. . . . . *persimplex*

50. Colour light brown. Postpetiole laterally with a broad, round expansion . (51)
– Colour dark brown or black. Postpetiolar lateral expansions pointed . . . (52)
51. Foveae of the cephalic disc contiguous. Vertex with a superficial depression. CI ≤ 100. PI < 104. Argentina. . . . . *pileini*
– Foveae of the cephalic disc separate by interspaces. Vertex without depression. CI = 113. PI = 113. Brazil, Argentina and Paraguay. . . . . *incertus*
52. Hind femora angulate . . . . . (53)
– Hind femora not angulate . . . . . (56)
53. Frontal carinae concolour with the rest of the head. Mexico to Argentina and Paraguay . . . . . *maculatus*
– Frontal carinae yellow, not concolour with the rest of the head which is dark brown to black . . . . . (54)
54. Foveae of the cephalic disc contiguous. Foveal hairs of the cephalic disc suberect . . . . . (55)
– Foveae of the cephalic disc separate by interspaces. Foveal hairs of the cephalic disc appressed. Mexico to Colombia, Venezuela and Ecuador . . . . *scutulatus*
55. Vertex with a very deep median depression. Brazil and Paraguay . . . . *pinelii*
– Vertex flat, without depression. Mexico, Belize, ?Costa Rica . . . . . *kukulcan*
56. Propodeal sides subconvex or with an obtuse medial tooth. . . . . (57)
– Propodeal sides with one or two pairs of teeth or denticles. . . . . (62)
57. First gastral tergite, anterolaterally, with a pair of yellow spots. . . . . (58)
– First gastral tergite, anterolaterally, without coloured spots . . . . . (61)
58. PPeI ≥ 247. Lower metapleurae with at least 60 appressed hairs. Costa Rica . . . . . *curvistriatus*
– PPeI < 239. Lower metapleurae with less than 35 appressed hairs . . . . . (59)
59. Foveae of the cephalic disc contiguous . . . . . (60)
– Foveae of the cephalic disc separate by interspaces. ?Guatemala . . . . *sobrius*
60. PPpI < 183. Postpetiolar expansions spiniform. Texas, North Mexico. *texanus*
– PPpI > 209. Pospetiolar expansions broad and obtuse. Mexico . . *bimaculatus*
61. Body sculpture less regular and very deep. HBaI (Hind Basitarsal Index) < 22. Arizona and North Mexico . . . . . *rohweri*
– Body sculpture more regular and superficial. HBaI (Hind Basitarsal Index) > 25. Mexico . . . . . *insularis*
62. Body covered with long, flexuous hairs. . . . . (63)
– Body without long, flexuous hairs, or if present, the flexuous hairs restricted to the sides of the head and to the border of the frontal carinae . . . . . (65)
63. Posterior third of the first gastral tergite with sparse punctuations and shining. Argentina. . . . . *liogaster*
– Posterior third of the first gastral tergite densely punctuate and opaque. . (64)
64. Anterior face of the petiole deeply concave. Ventral process of the petiole round and narrow. Argentina. . . . . *lanuginosus*
– Anterior face of the petiole only weakly concave. Ventral process of the petiole subtruncate and broad. Brazil, ?Argentina, Paraguay. . . . . *pilosus*
65. CI ≥ 112. HBaI (Hind Basitarsal Index) ≥ 38. Colombia. . . . . *patei*
– CI < 106. HBaI (Hind Basitarsal Index) < 35. . . . . (66)
66. Sides of the first gastral sternite with thin, longitudinal rugosities . . . . . (67)
– Sides of the first gastral sternite simply reticulate . . . . . (69)

67. Whole borders of the cephalic disc raised. Anterior third of the first gastral tergite with longitudinal rugosities . . . . . (68)
– Only the anterior part of the border of the cephalic disc raised. Anterior third of the first gastral tergite simply reticulate, without longitudinal rugosities. Brazil . . . . . *pallidicephalus*
68. Foveae of the floor of the disc deep and irregular. PPeI ≤ 250. PPpI ≤ 200. HBaI (Hind Basitarsal Index) < 25. Brazil . . . . . *notatus*
– Foveae of the floor of the disc shallow and regular. PPeI > 289. PPpI > 213. HBaI (Hind Basitarsal Index) ≥ 30 . . . . . *goeldii*
69. Sides of the frontal carinae and of the head bearing long, pointed, flexuous hairs. Argentina . . . . . *supercilii*
– Sides of the frontal carinae and of the head bearing clavate or truncate hairs . . . . . (70)
70. Posterior fourth of the head dorsum flat to gently convex, the rest concave . . . . . (71)
– Head dorsum uniformly flat, concave or convex. . . . . (72)
71. TL > 11 mm. CI > 103. PPeI < 224. HBaI (Hind Basitarsal Index) > 31. Argentina. . . . . *prodigiosus*
– TL < 9 mm. CI < 98. PPeI > 236. HBaI (Hind Basitarsal Index) < 22. Argentina . . . . . *bivestitus*
72. Distance between the eyes and the border of the disc shorter than the maximum diameter of the eyes . . . . . (73)
– Distance between the eyes and the border of the disc as long as or longer than the maximum diameter of the eyes . . . . . (75)
73. Foveae on the floor of the disc sparse. Ecuador . . . . . *ecuadorialis*
– Foveae on the floor of the disc dense and contiguous . . . . . (74)
74. PPpI < 195. Hairs on the anterior third of the first gastral tergite sparse. Colombia . . . . . *coffeae*
– PPpI > 210. Hairs on the anterior third of the first gastral tergite dense. Venezuela, Colombia . . . . . *crenaticeps*
75. Vertexal angles with a semitransparent lamella. Brazil. . . . . *frigidus*
– Vertexal angles simply marginate, without lamella. . . . . (76)
76. Border of the frontal carinae with short, truncate hairs. Argentina . . . . . *fossithorax*
– Border of the frontal carinae with clavate hairs . . . . . (77)
77. Foveal hairs of the cephalic disc appressed. Brazil and Argentina . . . . . *angustus*
– Foveal hairs of the cephalic disc subdecumbent or erect. . . . . (78)
78. PPeI < 197. PPpI < 170. Brazil, Paraguay . . . . . *guayaki*
– PPeI >226. PPpI ≥ 184 . . . . . (79)
79. Foveal hairs of the cephalic disc suberect to erect. Brazil, Argentina, Paraguay . . . . . *fiebrigi*
– Foveal hairs of the cephalic disc subdecumbent . . . . . (80)
80. Dorsum of the postpetiole with a V-shaped carina. Venezuela, Trinidad, Guyana, Brazil, Bolivia, Paraguay . . . . . *targionii*
– Dorsum of the postpetiole with a U-shaped carina. Brazil, Argentina, Paraguay . . . . . *jheringi*

5.8.4. Males

The following key to the males is very imperfect since males are known for only 48 species of *Cephalotes*. Because there are no previous examples of keys to the males of Cephalotini either for groups of species or for restricted faunas, we thought that our incomplete effort may nonetheless result of some use when isolate males are collected after the nuptial flight or at light. In some instances we have been already able to identify non female-associated males by means of the information contained in the following key.

The following 81 species, the male of which is still unknown, are not considered in the key:

adolphi, *alfaroi*, *argentiventris*, *auriger*, *betoi*, *biguttatus*, *bivestitus*, *bohlsi*, *bruchi*, *chacmul*, *complanatus*, *conspersus*, *cordatus*, *cordiae*, *cordiventris*, *crenaticeps*, *decolor*, *decoloratus*, *dentidorsum*, *ecuadorialis*, *emeryi*, *femoralis*, *flavigaster*, *foliaceus*, *fossithorax*, *frigidus*, *goniodontus*, *grandinosus*, *guayaki*, *hirsutus*, *inaequalis*, *inca*, *incertus*, *insularis*, *klugi*, *lenca*, *liepini*, *liogaster*, *manni*, *membranaceus*, *mompox*, *nilpiei*, *notatus*, *palta*, *palustris*, *patellaris*, *pavonii*, *persimplex*, *peruviensis*, *pileini*, *prodigiosus*, *quadratus*, *ramiphilus*, *resinae*, *simillimus*, *sobrius*, *solidus*, *spinosus*, *supercilii*, *taino*, *toltecus*, *trichophorus*, *ustus*, *vinosus*, *wheeleri*, †*alveolatus*, †*bloosi*, †*brevispineus*, †*caribicus*, †*dieteri*, †*hispaniolicus*, †*integerrimus*, †*jansei*, †*maya*, †*obscurus*, †*olmecus*, †*poinari*, †*serratus*, †*squamosus*, †*sucinus*, †*ventriosus*.

In addition to the above, the males of *patei* and *texanus*, described in the literature but not seen by us, are also excluded from the key. The male of *wheeleri*, described in the present paper on a single specimen is also not considered in the key because of the scarce reliability of all biometric characters we can draw from the unique immature specimen.

1. Propodeum with a pair of round or obtuse denticles or teeth; if denticles or teeth are missing (some specimens of *atratus*) size larger than 9.5 mm . . . (2)
– Propodeum unarmed . . . . . (9)
2. Vertexal angles with one or two denticles; if unarmed (some specimens of *atratus* and *marginatus*) size larger than 9.5 mm . . . . . (3)
– Vertexal angles without denticle(s) . . . . . (7)
3. First gastral tergite with sparse, long hairs. Distal part of the gonostyli truncate (Figs. 39, 41). Internal border of the aedeagus ventrally concave (Figs. 39, 41) . . . . . (4)
– First gastral tergite with rare, subtruncate hairs. Distal part of the gonostyli pointed (Figs. 51, 57, 61). Internal border of the aedeagus ventrally straight (Figs. 51, 57, 61) . . . . . (5)
4. CI > 127. Mesonotum with sparse foveae. Belize?, Virgin Islands?, from Costa Rica to Argentina . . . . . *atratus*
– CI < 123. Mesosoma densely covered by foveae. Guyanas, Colombia, Brazil . . . . . *marginatus*
5. PPeI < 191. PPpI < 178. Apex of the gonostyli broad (Fig. 57). Colombia, Venezuela, Guyanas, Brazil, Ecuador, Peru, Bolivia . . . . . *opacus*
– PPeI ≥220. PPpI > 192. Apex of the gonostyli narrow (Figs. 51, 61) . . . . (6)

6. Propodeal spines ca. 1/3 of the length of the basal face of the propodeum and subpointed. Colombia, Guyana, Brazil, Peru . . . . . *placidus*
– Propodeal spines very short and round. Brazil . . . . . *oculatus*
7. Body hairs ferrugineous brown. PPpI < 194. Dominican Republic . *auricomus*
– Body hairs yellowish to golden. PPpI > 206 . . . . . (8)
8. PPeI > 245. Dominican Republic, Haiti . . . . . *unimaculatus*
– PPeI = 225. Dominican Republic, Haiti . . . . . *hamulus*
9. Vertexal angles with a small pair of denticles. Brazil, Peru . . . . . *serraticeps*
– Vertexal angles without denticles or simply obtuse . . . . . (10)
10. Gaster heart-shaped . . . . . *umbraculatus*
– Gaster either oval or round . . . . . (11)
11. PPeI > 330. Dorsal border of the aedeagus bent ventrally with an angle of ca 90°. Aedeagus minutely denticulate on the distal border. Mexico, Belize, ?Costa Rica . . . . . *kukulcan*
– PPeI < 278. Dorsal border of the aedeagus normally curved ventrally. Distal border smooth . . . . . (12)
12. PeW > 0.85 mm . . . . . (13)
– PeW < 0.77 mm . . . . . (15)
13. CI = 139. Body foveae sparse, sculpture superficial. Sides of the peduncle foveolate. First gastral tergite with superficial reticulation. Distal projection of the aedeagus minutely denticulate (Fig. 89). Panama, Colombia, Venezuela . . . . . *christopherseni*
– CI < 135. Body foveae dense, sculpture impressed. Sides of the peduncle foveolate-rugulose. First gastral tergite with impressed reticulation. Distal projection of the aedeagus without denticles (Figs. 67, 69) . . . . . (14)
14. Head very broad (CI = 133). Scutellum posteriorly convex, not strongly narrowing posteriorly. Gaster without or only with few thin, longitudinal rugosities. Colombia and Venezuela . . . . . *columbicus*
– Head less broad (CI < 127). Scutellum subtriangular, i. e. strongly narrowing posteriorly. Gaster with thin, longitudinal rugosities. Colombia to Argentina and Paraguay . . . . . *pusillus*
15. TL > 9 mm. PpW > 0.90 mm. Pronotum and petiole densely covered by decumbent hairs hiding the sculpture. Colombia and Brazil . . . . . *duckei*
– TL < 8.7 mm. PpW < 0.84 mm. Pronotum and petiole not covered by hairs hiding the sculpture . . . . . (16)
16. PpW ≤ 0.31. Mexico to Paraguay . . . . . *maculatus*
– PpW > 0.35 . . . . . (17)
17. HBaL (Hind Basitarsal Length) ≥ 0.72 . . . . . (18)
– HBaL (Hind Basitarsal Length) ≤ 0.65 . . . . . (23)
18. PPeI < 164. PPpI < 148. Distal projection of the aedeagus with a group of denticles. Brazil . . . . . *laminatus*
– PPeI > 219. PPpI > 200. Distal projection of the aedeagus not denticulate (19)
19. Humeral angles with a broad lateral projection. Trinidad & Tobago, from Colombia to Argentina and Paraguay . . . . . *clypeatus*
– Humeral angles at most simply angulate . . . . . (20)
20. Petiole longer than high. Antennae longer than the sum of the head and mesosoma . . . . . (21)

– Petiole as long as high. Antennae shorter than the sum of the head and mesosoma . . . . . (22)

21. CI ≥ 139. PI > 114. Vertexal angles broadly obtuse. Mexico to Colombia . . . . . *cristatus*

– CI < 130. PI < 97. Vertexal angles almost round. Mexico, Costa Rica and Panama . . . . . *multispinosus*

22. PPeI > 264. Petiole narrower than the postpetiole. Petiole less than 1/3 broader than long. Mexico to Ecuador . . . . . *basalis*

– PPeI < 242. Petiole and postpetiole subequal in width. Petiole twice broader than long. Brazil, Peru, Bolivia . . . . . *cordiae*

23. CI > 134 . . . . . (24)

– CI < 131 . . . . . (27)

24. Head dorsum simply reticulate-punctate, without foveae. PpW = 0.40. PPeI = 250. PPpI = 250. Internal border of the aedeagus ventrally straight (Fig. 260) . . . . . *setulifer*

– Head dorsum foveolate. PpW > 0.56. PPeI < 234. PPpI < 201. Internal border of the aedeagus ventrally deeply concave (Figs. 152, 157, 163) . . . . . (25)

25. Maximum length of the first gastral tergite 1/3 to 1/4 longer than the summed length of the petiole and postpetiole. Digitus volsellaris short (Fig. 152). Brazil, Argentina and Paraguay . . . . . *borgmeieri*

– Maximum length of the first gastral tergite about 1/5 longer than the summed length of the petiole and postpetiole. Digitus volsellaris long (Figs. 157, 163) . . . . . (26)

26. Foveae on the mesosoma dense and deep. Petiole and postpetiole narrower (PeW 048–0.58 mm; PpW 0.56–0.67 mm). Venezuela to Bolivia, Argentina, Paraguay. . . . . *depressus*

– Foveae on the mesosoma sparse and shallow. Petiole and postpetiole broader (PeW 0.60–0.68 mm; PpW 0.68–0.76). Brazil, Bolivia, Argentina, Paraguay . . . . . *eduarduli*

27. PPpI < 156 . . . . . (28)

– PPpI > 161 . . . . . (30)

28. First gastral tergite shining and smooth. Brazil, Argentina and Paraguay . . . . . *persimilis*

– First gastral tergite opaque and reticulate. . . . . (29)

29. Petiole, postpetiole and anterior third of the first gastral tergite covered by thick rugosities. HBaI < 16. Distal projection of the aedeagus with a group of denticles (Fig. 82). Mexico to Argentina and Paraguay . . . . . *minutus*

– Petiole, postpetiole and anterior third of the first gastral tergite only with few, thin, rugosities. HBaI > 22. Distal projection of the aedeagus without denticles (Fig. 296). Brazil, Argentina, Paraguay . . . . . *jheringi*

30. Maximum diameter of the eyes at least 2/3 of the maximum head length (mandibles excluded). Brazil . . . . . *goeldii*

– Maximum diameter of the eyes less than 2/3 of the maximum head length (mandibles excluded). . . . . (31)

31. Mesosoma, pedicel and gaster, dorsally, completely shining and smooth. Venezuela, Trinidad, Guyana, Brazil, Bolivia, Paraguay . . . . . *targionii*

– Body mostly reticulate, never smooth, sometimes with superficially shining gaster only. . . . . (32)

32. PPpI > 241 . . . . . (33)
– PPpI < 230 . . . . . (34)
33. Humeral angles obtuse and laterally protruding. Internal, articulator, border of the aedeagus dorsally simply straight. Brazil . . . . . *pallidicephalus*
– Humeral angles only marked but not laterally protruding. Internal, articulator, border of the aedeagus dorsally narrowly concave. Costa Rica . . *curvistriatus*
34. Angle between the basal and declivous faces of the propodeum separate by a carina. Colombia . . . . . *coffeae*
– Angle between the basal and declivous faces of the propodeum not separate by a carina . . . . . (35)
35. Dorsum of the petiole and postpetiole covered with thick rugosities. Gonostyli very long, surpassing the median parameres of more than half of their length. Brazil and Paraguay . . . . . (36)
– Petiolar and postpetiolar dorsum at maximum covered with thin rugosities. Gonostylus short, surpassing the median parameres for less than half of its length . . . . . (38)
36. Gonostyli very hairy (i. e. with > 20 hairs visible on the profile) . . . . . (37)
– Gonostyli only sparsely hairy, i. e. with <10 visible hairs on the profile. Brazil, Argentina, Paraguay . . . . . *fiebrigi*
37. Eyes larger (EL 0.48 mm), petiole and postpetiole broader (PeW ≥ 0.64 mm; PpW = 0.63 mm). Argentina . . . . . *lanuginosus*
– Eyes smaller (EL ≤ 0.44 mm), petiole and postpetiole narrower (PeW ≤ 0.54 mm, PpW ≤ 0.58 mm). Brazil, Paraguay, ?Argentina . . . . . *pilosus*
38. Maximum pronotal width slightly broader than the width of the head . . (39)
– Maximum pronotal width as broad as or narrower than the head width. . (40)
39. TL > 5 mm. PI > 95. Internal border of the aedeagus straight . . . . . *angustus*
– TL < 4.8 mm. PI < 87. Internal border of the aedeagus, medially, with a remarkable projection . . . . . *scutulatus*
40. Gaster completely smooth and shining . . . . . (41)
– Gaster variably reticulate and subopaque. . . . . (42)
41. Gonostyli very hairy (i. e. with > 35 hairs visible on the profile). Mexico to Ecuador . . . . . *porrasi*
– Gonostyli with less hairs (i. e. with < 27 visible hairs on the profile). Florida, Bahamas, Cuba . . . . . *varians*
42. Foveae on the mesosoma contiguous. Dorsal border of the aedeagus in form of a continuous curve. Apical tooth of the aedeagus absent or indistinguishable. Brazil and Paraguay . . . . . *pinelii*
– Foveae on the mesosoma sparse. Dorsal border of the aedeagus forming an angle. Apical aedeagal tooth well visible . . . . . (43)
43. Frontal carinae high and broadly convex. Gonostyli apically narrow and pointed (Fig. 221). Guyana, Surinam, Brazil and Bolivia . . . . . *pallidus*
– Frontal carinae low, weakly protruding. Gonostyli apically broad and obtuse or round (Figs. 224, 234, 238). . . . . (44)
44. Petiole and postpetiole very narrow (PeW = 0.31 mm; PpW = 0.36 mm). Mexico to Brazil. . . . . *pallens*
– Petiole and postpetiole broad (PeW ≥ 0.39 mm; PpW ≥ 0.43) . . . . . (45)
45. Subgenital plate with less than 45 hairs. Brazil, Bolivia and Paraguay. . *pellans*
– Subgenital plate with more than 60 hairs. Venezuela, Trinidad, Guyana, Brazil, Bolivia . . . . . *pallidoides*

5.9. Species described in *Cephalotes* (or its synonyms) and transferred to other genera

Cryptocerus bicolor GUÉRIN-MÉNEVILLE, 1845: 425. Worker. India.
= *Meranoplus bicolor* (GUÉRIN-MÉNEVILLE). Generic transfer by SMITH, 1854: 224.

Cryptocerus pubescens SMITH, 1854: 224. Gyne. Australia.
= *Meranoplus pubescens* (SMITH). Generic transfer by DE DALLA TORRE, 1893: 137.

Cryptocerus? rimosus SPINOLA, 1853: 65. Worker. Pará (Brazil).
= *Cyphomyrmex rimosus* (SPINOLA). Generic transfer by DE DALLA TORRE, 1893: 150.

Paracryptocerus Mayri Reichenspergeri SANTSCHI, 1921 a: 98. Worker. Brazil.
= *Procryptocerus mayri* ssp. *reichenspergeri* (SANTSCHI). Generic transfer by KEMPF, 1951: 105.

5.10. Invalid names referable to *Cephalotes*

The following names referred to *Cephalotes*, by being not available for nomenclatorial purposes, cannot be included within the appropriate synonymies of the various species.

Cephalotes atratulus (sic) L., SANTSCHI, 1929: 303. Incorrect spelling for *atratus*.

Cephalotes atratus quadridens var. *dehnowi* FOREL, 1922: 97. Worker. Original description. Type locality: South America. Type material worker (unique) with only 4 legs and partially broken gaster, labelled "Amérique" in MHNG, examined. Unavailable name (quadrinomen). Identity with *atratus* suggested by KEMPF (1951: 115) and confirmed by our examination of the type material.

Cephalotes atratus quadridens var. *erecta* SANTSCHI, 1920: 149. Worker. Original description. Type locality: Darien (Panama). Type material 2 syntype workers labelled "Darien, F. Geay, 33–96", in NHMB (examined). Unavailable name (quadrinomen), made available as trinomen by KEMPF, 1951. See under *atratus*.

Cryptocerus curvispinosus ROGER, MAYR, 1863: 459. St. Domingo. *Nomen nudum*.

Cryptocerus guttatus (sic) SANTSCHI, 1929: 301. Incorrect spelling for *guttifer*.

Cryptocerus maculatus var. *cearensis* FOREL, 1908 b: 69. *Nomen nudum*.

Cryptocerus multistrigus SM., ASHMEAD, 1905: 384. *Nomen nudum*.

Cryptocerus peltatus Ellenriederi var. *gaudens* SANTSCHI, 1922: 255. Worker and soldier. Original description. Type locality: Alta Gracia (Córdoba, Argentina). Type material: 13 workers, 4 soldiers, 2 gynes (syntypes), first label "Córdoba, Alta Gracia, Bruch", second label "branches de cocos", third label "*C. peltatus* Em., *ellenriederi* For., v. *gaudens* Sant., type", in NHMB, examined. Unavailable name (quadrinomen). Identity with *jheringi* suggested by KEMPF (1958 a: 50) and confirmed by our examination of the type material.

Cryptocerus peltatus Ellenriederi var. *jocans* FOREL, 1913 b: 235. Soldier. Original description. Type locality: Catamarca (Argentina). Type material: holotype soldier, first label "*Cr. peltatus* r. *Ellenriederi* For., v. *jocans* For., type, Catamarca, Arg.,

Bruch" (handwriting of Forel), second label "Rca. Argentina, Prov. Catamarca, 185, C. Bruch" (printed), in MHNG, examined. Unavailable name (quadrinomen). Identity with *jheringi* suggested by KEMPF (1958 a: 50) and confirmed by our examination of the type material.

Cryptocerus peltatus Ellenriederi var. tucumana FOREL, 1914: 281 (in part). Worker. Original description. Type locality: Tucumán, Argentina. Type material. 2 workers on the same pin (upper worker = *bivestitus*, lower worker = *fiebrigi*), labelled "Tucumán, Shipton leg., *Cryptocerus peltatus* Em. r. *Ellenriederi* For. v. *tucumana* For., worker, type", in MHNG, examined. Unavailable name (quadrinomen). Identity with *bivestitus* proposed by KEMPF (1958 a: 50) and confirmed by our examination of part of the relevant material.

Cryptocerus pusillus var. *brevispinosa* ab. *rufescens* SANTSCHI, 1921 b: 127. Worker. Original description. Unavailable name (quadrinomen). Type locality: Chaco (Argentina). Type material: holotype worker, first label "Argentine, Gr. Chaco, (v. Steiger)", second label "*Cryptocerus pusillus* Klug. aberat., *f* Santschi det 19" in NHMB (examined). Identity with *pusillus* suggested by KEMPF (1951: 176) and confirmed by our examination of the type material.

Zacryptocerus christophersoni (sic) (FOREL), HESPENHEIDE, 1986: 395. Incorrect spelling for *christopherseni*.

6. Some biological traits of *Cephalotes* of probable relevance in understanding its diversity and adaptations

It is probable that at least some of the peculiarities summarised in the following for *Cephalotes* should be extended to the whole tribe Cephalotini and also apply to *Procryptocerus*. We shall focus our discussion, partly based on a literature compilation, on the traits most likely to affect or to be correlated with *Cephalotes* speciation, diversity and bizarre morphology.

Cephalotes species exhibit several uncommon adaptations to arboreal life and to passive avoidance of predators. In spite of their partial loss of the nest digging behaviour (as far as it is known all species nest in pre-existing cavities), these ants possess a very rich behavioural repertoire.

In a study on behavioural complexity of ants, based on nine species including *C. varians*, COLE (1985) stresses that *C. varians* possesses the most diverse ant behavioural repertoire known so far. COLE (l. c.) explains this feature by assuming that behavioural complexity in ants should be related to the cube of head width, which, in turn, should be an allometric function of brain volume. As a matter of fact, brain volume is unknown in *C. varians*, and *Cephalotes* species characteristically have a very broad but also very flattened (i. e. with reduced capacity) head. In the following, we shall provide some circumstantial evidence for homogeneity of behaviour within most *Cephalotes* species in spite of their manifold differences in head width. A similar correlation between brain volume and what he called "psychic capacities" of ants had been already postulated by FOREL (1902). We suspect that the correlation between head width and behaviour may be too trivial to explain ants' behavioural complexity over a broader sample of species. Several ant species appear to have very broad heads essentially to host powerful mandibular muscles. GRONENBERG (1996) has recently considered a narrower form of correlation between ant behaviour and size of certain brain parts.

The fact that most species of *Cephalotes* are behaviourally and ecologically rather uniform suggests that the adaptive strategy they share is a rewarding one. And this reward is corroborated by the contrast between their behavioural uniformity and their morphological diversity.

In the following pages we shall describe some ecological, behavioural and morphological parameters associated with apparent disparity between taxonomic radiation and biological uniformity which characterises these ants. Among the presumably most significant features of *Cephalotes* we have been able to accumulate in this context are the following: massive polyandry, a diet based largely on virtually unlimited food resources, a unique combination of multiple adaptations to passive defence, and a high rate of spontaneous mutation.

6.1. Nest demography

The first information on *Cephalotes* nest location and nest composition comes from a paper by SMITH (1876) who states "that *Cryptocerus* constructed its burrows in decaying trees, its colonies not being numerous; consisting, in the nests examined, of about a dozen females, a few males, and the workers, numbering about the same as the females". These improbable statements must not, however, be attributed to FREDERICK SMITH, who is indebted for his information to no less a famous observer, explorer and collector in Amazonia than HENRY W. BATES. Equally doubtful is a statement by ALLEE et al. (1949: 425) for which "each colony of *Cryptocerus*... contains only one or two soldiers".

In fact, the adult nest population of *Cephalotes* seems to be inter- and intraspecifically very variable. Just to give an example, individual mature colonies of *C. atratus* have been reported to contain a single queen, 83 workers, 50 eggs, 364 larvae and 36 pupae in S. Brazil (EIDMANN, 1936), a single queen, 10223 adult workers, 94 adult males, 1086 worker pupae and 48 male pupae in Trinidad (WEBER, 1957), and one queen and 2533 workers in Colombia (CORN, 1980) but the same author (CORN, 1976) estimates the population of another colony of the same species at over 100,000 workers. Nests of *C. pinelii* in Brazil have a population varying between 30 and 100 workers (LUEDERWALDT, 1925). CREIGHTON & GREGG (1954) give adult nest populations varying between 29 and 232 individuals for *C. texanus* in Texas and in Nuevo León, and refer of a single Mexican nest of *C. cristatus* containing 338 adult workers. A Brazilian colony of *C. pusillus* is reported to contain 129 adult workers (FERNANDES et al., 1989), though this low figure is likely to be explained by the fact that the authors probably inspected a single cali of a polycalic colony. Nest populations of *C. rohweri* in Arizona are much smaller, since they seldom comprise more than 75 workers and most of the colonies contain less than 50 individuals (CREIGHTON & GREGG, 1954). *C. christopherseni* colonies contain over 4000 workers (WHEELER, 1984). WILSON (1976 b) states that mature colonies of *C. varians* in Florida may contain from one to several hundreds of workers. One of us (CBU), marked 90 individuals from a nest of *C. minutus* near H. Cárdenas in the Mexican state of Tabasco and made 8 successive recaptures of marked workers over 14 days. Calculation of the total population by the Petersen-Bailey Index gave a worker population estimate varying between 257 and 797 workers. The limits of this method are summarised by BARONI URBANI et al. (1978). Accepting the assumption that, in this way, one is likely to actually estimate only the worker sub-population devoted to collecting food, the above figures should be subject to a ten-fold

magnification to extrapolate the total worker population. In the course of the present study we made nest population counts in the following situations:

1. A large queenless fragment of a Brazilian colony of *C. pusillus* from Botucatu (S. Paulo) available for the present study and already mentioned in the Materials chapter, contained several pre-imaginal stages, 552 soldiers and 1862 workers (neuter, i. e. soldier: worker, ratio = 1 : 33).

2. A large queenless fragment of a colony of *C. borgmeieri* from Lins (S. Paulo) with 177 workers, 6 worker pupae, 45 soldiers, 20 winged gynes, 3 gyne pupae, 43 males, 13 male pupae (neuter, i. e. soldier : worker, ratio = 1 : 4; secondary sex ratio = 10 : 4).

3. A queenless large fragment of a colony of *C. clypeatus* from Lins (S. Paulo) comprising 355 workers, 21 soldiers, 66 males and 18 winged gynes. Neuter, i. e. soldier : worker, ratio = 1 : 16.9; secondary sex ratio = 3.6 : 1.

4. A presumably complete nest of *C. angustus* from Botucatu (S. Paulo) which contained 2 dealate gynes, 8 eggs, 73 larvae of different ages, 24 worker pupae, 8 soldier pupae, 2 gyne pupae, 7 male pupae, 450 workers, 169 soldiers, 36 winged gynes and 7 males. This nest was collected at the end of January, i. e. shortly after the main swarming season of most ants in the state of S. Paulo. For this reason we don't trust the sex ratio derived from the few males and gynes collected. The neuter (soldier : worker) ratio is 1 : 2.7.

5. A presumably complete nest of *C. auricomus* collected in a dead branch of a tree close to Puerto Plata (Dominican Republic) on June 2, 1995. It contained one queen, 520 eggs, 192 larvae of different ages, 69 worker pupae, 10 gyne pupae, 75 male pupae, 483 workers, 24 gynes, and 151 males. We suppose, however, that at least 5% of the population (particularly males which flew away) may have been lost during the nest dissection in the field. Summing all the adults and pupae of the same sex or caste give a male-biased secondary sex ratio of 10 : 1.

Since most *Cephalotes* species are probably monogynous, kin selection theory (see e. g. TRIVERS & HARE, 1976) predicts that such a high male investment should be possible only if the queen had multiple matings with several males. And, of course, such strongly male-biased sex ratios, are destined to further increase polyandry.

6.2. Ecological requirements and natural density

Abundant, but often anecdotal, evidence suggests that all species of *Cephalotes* should be arboreal or living in shrubs, or even in grass stems (e. g. FOREL, 1899 a; COLE, 1982; FERNÁNDEZ & SCHNEIDER, 1989; etc.). BATES (1863) reports collecting 15 different species in Amazonas, all inhabiting hollow twigs or the branches of trees. EIDMANN (1936) stresses the abundance of *C. pusillus* in S Brazil and gives a detailed description of a nest in hollow twigs. JEANNE (1979) observed species of this genus at frequencies of between 3 and 5 % of the ants predating on baits over leaves, under tree canopy and among canopy trees (at 15 m height) in Costa Rica and in Brazil. ADIS et al. (1984) give frequencies of between < 0.1 and 6.2 % of the total ant population for *C. atratus*, *C. serraticeps* and three undetermined species collected by canopy fogging in three forest types close to Manaus, Brazil. ZENNER-POLANIA (1994) gives frequencies of ca. 0.5% of the ant population for each, *C. atratus*, "*Eucryptocerus*" sp. and "*Zacryptocerus*" sp. in undisturbed habitats in Colombia. FERNÁNDEZ & SCHNEIDER (1989), in their survey of the ants of the reserve "La Macarena" in Colombia, also recorded *C. atratus* exclusively from gallery forests. These results conflict somehow with those of LESTON (1978) who reports *C. atratus*

to be numerically dominant in a secondary forest near Bahia (Brazil) and those of JAFFE et al. (1986) (for Venezuelan cacao plantations) where they record the presence of three *Cephalotes* species (out of 68 ant species) with *C. atratus* as the third (or second?) most abundant species after *Azteca foreli* and *Crematogaster* sp. These scattered observations could indicate a greater ecological success for *C. atratus* in disturbed habitats. Analogously, MAJER & DELABIE (1994) record two species of "*Zacryptocerus*" in transects of flooded Brazilian Amazonian forest, one from lowland forest but none from upland forest.

Plants appear to represent the ideal if not the obligatory nesting site for *Cephalotes* and WHEELER (1942) provides a complete list of plants associated with those Cephalotini known at the time of the publication of his paper. The majority of these records refer to domatia-bearing plant genera, like *Cecropia* and *Cordia* or to *Acacia* where the colonies are hosted in thorns. There are no definite indications of symbiotic relationships between any cephalotine species and these plants as is the case for other ants (BEATTIE, 1985). There are some cases of *Cephalotes* being reported to nest in the internodes of *Cecropia*, as one would expect from true symbionts (MÜLLER, 1881; WHEELER & BEQUAERT, 1929; BROWN, 1957). LONGINO (1989), who observed similar associations in Costa Rica, defines the presence of *Cephalotes* in *Cecropia* as "non-obligate". Similarly, RICO-GRAY (1987) lists *Cephalotes maculatus* as one of the rarest of the 13 ant species associated with the orchid *Schomburgkia tibicinis* in Yucatan. Some *Cephalotes*, however, are frequent inhabitants of the epiphytic "ant gardens" of orchids or of *Tillandsia*, but none has been recorded exclusively on epiphytes and frequently enough as to suggest obligatory relationships (SKWARRA, 1934). One species (*C. patei*) has been collected only in New Jersey quarantine stations from orchids imported from Colombia (KEMPF, 1951) and the limited information available on another (*C. setulifer*) suggests that it could be an obligatory inhabitant of the cauline swellings of *Cordia alliodora* (KEMPF, 1958 a).

From a graph presented by CARROL (1974), one can deduce that *C. pallens* is the second most abundant ant species (after *Pseudomyrmex gracilis*) encountered in tree stems from two forest types in Costa Rica and that in a lowland riparian forest it is about twice as numerous as in the upland forest. WHITCOMB (1980) lists one or more unidentified species of *Cephalotes* among the numerically dominant ants of the swampy area of Pantanal in Brazil. FOWLER et al. (1994), using baits of an unprecise nature, recorded the regular presence of 2–3 *Cephalotes* species in different undisturbed habitats of the São Francisco River Valley (between the states of Bahia and Pernambuco, Brazil). *C. pusillus* can be encountered in different agricultural ecosystems of the state of Minas Gerais in Brazil but it occurs in significant quantities only in the "cerrado" (CASTRO & QUEIROZ, 1987). Subsequently, CASTRO et al. (1990) report the same species in the same state as being among the numerically dominant ants in absolute terms, of all those collected in two different environments by means of canned sardine baits. *C. atratus* has been observed nesting in a wide variety of trees but never in *Acacia* or in palm trees (CORN, 1976). Most *Cephalotes* species, however, are rare, and even common species able to monopolise one or more trees are seldom represented by great numbers of nests per area. CORN (1976) estimates the natural density of *C. atratus* in the Colombian "llanos" at ca. 175 nests per km^2, a very low density if one considers the few competitors and predators this species has. CORN (l. c.) suggests that this incongruence may be explained by a much higher predation rate during the nuptial flight and on isolated founding queens.

Though species of *Cephalotes* are proper inhabitants of the neotropical forests, their nest requirements appear to be often simple and they are commonly found nesting in dead branches, hollow twigs, and even in oak galls (LONGINO & WHEELER, 1987), galls produced by beetles of the genus *Apion* (ARAÚJO et al., 1995), and leaf-bud galls (FERNANDES et al., 1989). We interpret a recent report by MAJER et al. (1997) of *C. atratus* and another *Cephalotes* species near *pallens* in forest litter samples from Bahia as occasional and not representative of the ecological requirements of these ants.

According to CREIGHTON (1963), *C. texanus* does not dig its nest in the wood but uses already available tunnels excavated by beetle larvae. There are presumptive reasons to believe that this should be the case for other species as well, such as those the nests of which are illustrated by BRUCH (1923). We observed similar nests of *C. minutus* in the Mexican state of Tabasco and of *C. angustus* in the Brazilian state of S. Paulo, though the presence of numerous particles of wood under the nest entrance suggest that the available cavities had been partly re-worked by the ants. For *C. atratus*, CORN (1976) states that "the nests occurred in trees which had to be hollowed out by the ants themselves".

For all these reasons, species of the genus can be collected even in severely disturbed habitats, like isolated trees in towns or in gardens. Most *Cephalotes* species, however, are to be found in the Neotropical arboreal zone, a zone which should be characterised by high individual ant density and by relatively low species diversity (see review and discussion in DAVIDSON, 1997). This empirically derived rule condemning *Cephalotes* to a limited species richness seems not to apply: any random sample of Neotropical forest has a probability of containing a new *Cephalotes* species equal to the probability of containing an already described one. This situation can be exemplified by the numerous undescribed species intercepted by plant quarantine stations in the U. S. and by our own field work and laboratory-examined material. In fact, *Cephalotes* has been already listed by VERHAAGH (1990) as one of the 10 most species-rich ant genera in the Peruvian rain forest.

6.3. Feeding habits

It has been already hypothesised that the peculiar morphology of the proventriculus described for the Cephalotini along with the presence of micro-organisms in the ileum should be correlated with some unique feeding habit (HÖLLDOBLER & WILSON, 1990: 556). In fact, the ant literature contains only limited evidence confirming this point of view. On the contrary, several observations appear to conflict with it. In short, morphological studies failed to attribute to the cephalotine proventriculus a pump-filtering function different from the proventriculi of other ants; microbiologists proved the ilean bacteria to be unable to digest any presumed "typical" cephalotine food; and most field observations listed different species of *Cephalotes* as unspecialized scavengers and/or feeders of homopteran secretions, two food sources shared with many other ant species. During the present study we succeeded in adding further information on this theme as well as synthesising data and in putting together data already available. A brief summary of these results has been published (BARONI URBANI & DE ANDRADE, 1997). Below, we give more details about the unique feeding habits and associated mechanisms of *Cephalotes*. These results are likely to apply to all Cephalotini.

6.3.1. Food preferences

The first portrayal of *Cephalotes* feeding habits dates back to LUND (1831), an entomologist properly famous more for the flavour than for the accuracy of his descriptions. In his paper he states that these ants have solitary habits and that they are predators behaving exactly as spiders do. LUND (l. c.) adds candidly: "je fus souvent trompé par l'apparence, et je pris ces animaux pour des araignées". The explanation for these observations can be found in a short remark by the arachnologist E. SIMON (in EMERY, 1890: 68, footnote): " Les Fourmis de ce genre ressemblent d'une manière frappante aux Araignées du genre *Aphantochilus* Cambr. (famille des Thomisidae)" (see also OLIVEIRA & SAZIMA, 1984, figs. 1–5). If one supposes that LUND mistook spiders for ants and not the other way around, then their presumed solitary and predatory habits are easily explained. The observations of LUND have been reported again by SMITH (1853 and 1876) who never saw a *Cephalotes* alive and yet nonetheless added of his own accord that the ants capture their prey "by springing upon it".

MANN (1916) observed *C. atratus* in Brazil eating a variety of garbage including carrion. This observation is confirmed by CORNABY (1974) who lists "*Paracryptocerus* sp." (later identified by us as *C. cordiventris*) among the insects feeding on dead lizards in Costa Rica. LUEDERWALDT (1925) appears to be the first to report *C. pusillus* feeding on bird excrement. According to WEBER (1957) the main source of food for *C. atratus* in Trinidad are the secretions of membracids; secondary sources are insect remains collected particularly from bird faeces. These observations are confirmed and completed by CORN (1976) who studied this species during 18 months in Colombia: she summarises that a variety of arthropods and even dead vertebrates are regularly consumed by *C. atratus*, but bird droppings are also visited regularly, though probably for their organic waste content and not for nitrogen; the main source of carbohydrates is said to be either extrafloral nectaries (the sole natural food source that CORN observed for the closely related *C. placidus*) or homopteran excreta, depending on local availability. According to DELABIE (1990) *C. atratus* also chews the bark of buds or shoots. JEANNE (1979) collected *Cephalotes* spp. by means of wasp larvae baits and wasp larvae are said to constitute a natural food source for *C. atratus* in Trinidad by FOREL (1912). LEVINGS (1983) reports collecting *C. atratus* and *C. umbraculatus* on the ground by means of tuna fish baits in Panama and CORTÉS LOPES & LEAL (1991) similarly report of "*Zacryptocerus* sp." on sardine baits. OLIVEIRA (1988) observed *C. pusillus* as being the most frequent ant visiting extrafloral nectaries during daytime in the Brazilian "cerrado". GALLARDO (1915) was able to maintain a laboratory colony of *C. jheringi* on a strict sugar diet: the ants regularly refused offers of insects. More precise information about the natural feeding habits of *Cephalotes* spp. comes from WHEELER & BAILEY (1920) who, by dissecting the infrabuccal pellets of *C. multispinus* from Guatemala, found scanty fragments of insect tissue, abundant fragments of plant tissue, and fungal spores in variable quantities: from infrequent to forming a considerable fraction of the total volume of the pellet. Dissections of the stomachs of *C. minutus*, *multispinus*, and *varians* larvae allowed these same authors to conclude that "the larval stomach is voluminous and closely packed with coarse chitinous fragments of small insects, in some cases interspersed with numerous fungus spores". FERNÁNDEZ & SCHNEIDER (1989) tabulate eight species of Cephalotini they observed in the reserve "La Macarena" (Colombia) as omnivorous.

All these observations contrast at least in part with the results of laboratory studies by CREIGHTON (1963), later confirmed by field studies (CREIGHTON, 1967), which showed that *C. texanus* accepts freshly killed insects and sugared substances – as most ants do – but regularly feeds on pollen, a fact reputed to be unique among all ants so far (HÖLLDOBLER & WILSON, 1990: 556). As a matter of fact the ant literature contains at least two additional records of pollen eating ants: members of the subfamily Pseudomyrmecinae (WHEELER & BAILEY, 1920; see also later, the footnote to chapter 6.3.3), and the formicine *Polyrhachis vicina* (WANG & TANG, 1994). WILSON (1976 b) reports that *C. varians* refuses pollen of *Lilium* but this result has only limited implications since CREIGHTON (1963) described earlier how *C. texanus* is strongly attracted by *Quercus* and *Acer* pollen but refuses that of *Mahonia*. CREIGHTON (1967) went even further and extrapolated that *C. texanus* depends strongly on oaks for pollen but does not need to nest in oak trees: any tree species is suitable for *C. texanus* survival provided that it is close to oaks and that it hosts epiphytes of the genus *Tillandsia*. The leaves of *Tillandsia* are covered by semi-erect scales which trap oak pollen grains that then can be easily collected by the ants.

In the Brazilian State of São Paulo TECH DOS SANTOS et al. (1993) record *C. pusillus* among the frequent, although numerically rare, visitors of the flowers of the ornamental leguminose *Bauhinia variegata* L. which is of oriental origin.

We maintained for a few months a large fragment of a natural colony of *C. pusillus*, small fragments of colonies of *C. atratus* and more or less complete colonies of *C. clypeatus*, *pallens*, *targionii* and *borgmeieri* in the laboratory. Among the different foods we offered, the ants showed a restricted interest only for certain sugary substances and particularly for diluted honey. They regularly refused a variety of other sweet liquids at different concentrations and – except for *clypeatus* – also freshly killed arthropods. After weeks of food deprivation, however, the ants accepted a broader spectrum of sweet substances, though never recruiting other workers to these food sources. But the foraging workers regularly exhibited a strong interest for a variety of cut branches from different trees we presented them with. The ants actually searched for pollen on the leaves and patrolled them as previously described by CREIGHTON (1963) for *C. texanus.* Other offers of pollen from different plant species available in Basle in winter and from some commercial flowers bought in flower shops were also accepted. Microscopic examination of workers of *pusillus* and *clypeatus* returning to the nest after such "leaf inspections" showed that they were carrying pollen grains in the mouth (Fig. 345). All ants accepted cooked ham: *clypeatus* and *borgmeieri* recruited very efficiently to it while the other species showed only a moderate interest for it and no species, except *atratus*, paid the slightest attention to dry pollen pellets which had been kneaded by honey-bees (essentially grass pollen).

In fact, the easiest way to discover a number of *Cephalotes* species under natural conditions is precisely by locating such leaf patrolling workers. We observed this behaviour frequently among a number of species including the less specialised *auricomus* in the Dominican Republic.

YURMAN & DOMINGUEZ-BELLO (1993) studied the bacterial flora of the intestine of *C. atratus* and *C.* near *pusillus*. They report bacterial densities of 10^5 bacteria per gram of digestive tissue. The numerically dominant bacteria are unidentified Gram-positive Coccobacilli and none of the observed bacteria showed either cellulolytic or uricolytic activity. The intestinal bacterial flora also differs between the two species

Fig. 345. *Cephalotes pusillus* (KLUG) soldier collected on its way back to the nest after visiting flowers of *Corylus avellana* in the laboratory. Ventral view of the mouthparts showing the pollen grains carried by means of curved bristles on the internal side of the mandibles and on the ventral side of the labium.

with respect to the relative proportions of the different bacterial types. In addition, YURMAN & DOMINGUEZ-BELLO (l. c.) report the presence of individual bacteria-free ants.

These results partly conflict with reports in the literature of *Cephalotes* feeding on bird droppings since uricolytic bacteria would be expected in such cases, unless – as already suggested by CORN (1976) – the ants explore the bird faeces only for insect remains. The absence of cellulolytic bacteria do not conflict with their hypothesised digestion of pollen. Cellulose in the pollen wall is present only in the inner layer, the intine (STANLEY & LINSKENS, 1974). Further, insects eating pollen usually feed on it for its protein content and the pollen grains need not even be crushed: digestion can take place through the micropylar membrane as has been shown for the honey-bee by WHITCOMB & WILSON (1929).

We dissected the intestines (essentially mid- and hindguts) from one dead worker of each of the following species obtained from entomological collections: *atratus*, *borgmeieri*, *clypeatus*, *pusillus*, *unimaculatus*, *Procryptocerus* sp., all from Brazil, except *unimaculatus* (from the Dominican Republic). Only in the gut of *clypeatus* did we find definite remains of pollen grains (probably Chenopodiaceae). None of the intestines dissected contained identifiable insect remains, but, in *atratus* there were a few unequivocal, undigested plant tissue fragments.

6.3.2. The most specialised insect proventriculus

Despite fragmentary anatomical, histological and behavioural information, multiple references in the literature to the peculiarities of the cephalotine proventriculus (most of them second-hand) failed to produce a comprehensive account of its functional morphology.

The bizarre structure of the cephalotine proventriculus was first described by FOREL (1878) who, by simple dissection of two specimens of *C. atratus*, sketched accurately the main morphological features of this organ, stressing its unique mushroom-like morphology coupled with the presence of star-shaped and lamelliform cuticular folds. EMERY (1888) emphasised the pump function of all ant proventriculi; this function had been already convincingly demonstrated by FOREL (1874) but EMERY (l. c.) proposed the term "Pumpmagen" for all ant proventriculi and provided a description of the proventriculi of six cephalotine species. For *C. atratus* he also succeeded in making serial sections allowing a first histological description of the connective and muscular tissues composing the organ and he re-described the cuticular folds already described by FOREL as broom-shaped projections („besenförmigen Fortsätze"). To better observe the latter, he had to clean them from what he thought to be the dry content of the stomach. However, the presence of connective tissue in the *Cephalotes* intestine has not been confirmed by subsequent studies and we will show that what EMERY interpreted as being dry stomach content is very likely to be a cuticular structure unique to *Cephalotes*. If EMERY's (1888) interpretation of some structures appears partly incorrect today, it is worth recalling that his paper still represents the main source of information on cephalotine proventriculi and that he performed histological studies on dry specimens relaxed in water and cleaned with a weak lye solution.

The first to observe a cephalotine proventriculus using modern methods and to describe in detail its histological structure is DEMOSS (1973) for *C. texanus*. However, his paper makes no mention of the presence of cuticular projections and the proventriculus of *C. texanus* is regarded as specialised within the Myrmicinae because of the presence of sieves although the author attributes no unique cephalotine characters in it. On the contrary, the main conclusion is misleading since it is repeatedly stated that the proventriculi of five myrmicine genera (*Trachymyrmex*, *Acromyrmex*, *Atta*, *Strumigenys* and "*Cryptocerus*") "are so similar that they cannot be distinguished one from the other with any degree of accuracy".

The sole available pictures of *Cephalotes* proventriculi have been published in a paper by CAETANO (1984) where a short morphological description of the proventriculi of *C. atratus* and *C. pusillus* is complemented by drawings and by a photographic documentation of histological preparations. In this paper, the difference between the alimentary canal of *Cephalotes* and that of two other myrmycine genera studied (*Atta* and *Solenopsis*) is emphasised. Among other results, the presence of the cuticular projections on the bulb (called "espinhos arborescentes") is confirmed and these structures are visible in several micrographs. Another important feature appearing for the first time in the pictures published by CAETANO (1984) (see his figs. 16 b, 17 c) is that, at least in *C. pusillus*, the bulb appears to be largely covered by a cuticular sheath. We think it very probable that this sheath corresponds to the "dry food" that EMERY had to remove in order to see the broom-shaped projections.

In the course of the present study we examined fresh proventriculi of the species listed below:

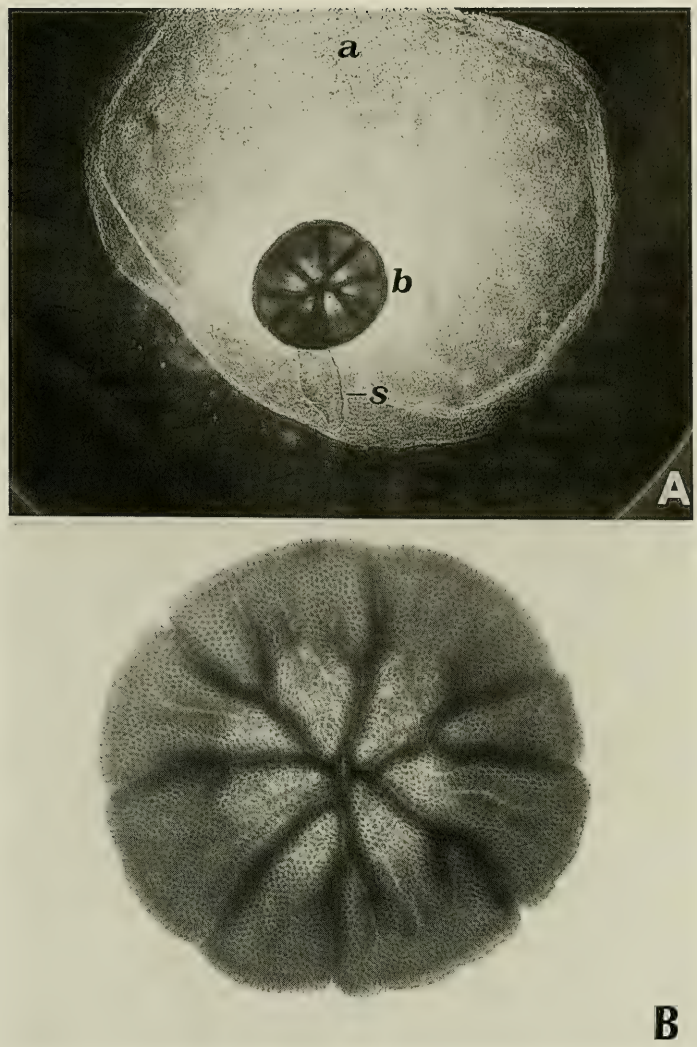


Fig. 346. *Cephalotes atratus* (LINNAEUS). A: dark field micrograph of the interior of the crop (*a*) showing the location of the bulb of the proventriculus (*b*) at its caudal end and the stomodeal valve (*s*), seen transparently through the crop wall. B: anterior view of the proventricular bulb showing its partition into irregular septa.

by simple dissection: *atratus*, *auricomus*, *borgmeieri*, *clypeatus*, *pusillus*, *unimaculatus*, *Procryptocerus* sp.

by serial cutting: stained preparations of *auricomus*, *clypeatus*, *pusillus*.

by scanning electron microscopy: *auricomus*, *atratus*, *borgmeieri*, *pusillus*.

Observation of all these species revealed a substantially similar morphological pattern that we can summarise as follows:

The bulb of the proventriculus lies at the bottom of the crop (Fig. 346, A) and it extends to the midgut with the cylinder. The bulb itself is like the umbrella of a mushroom in shape and is covered by a transparent integumental framework

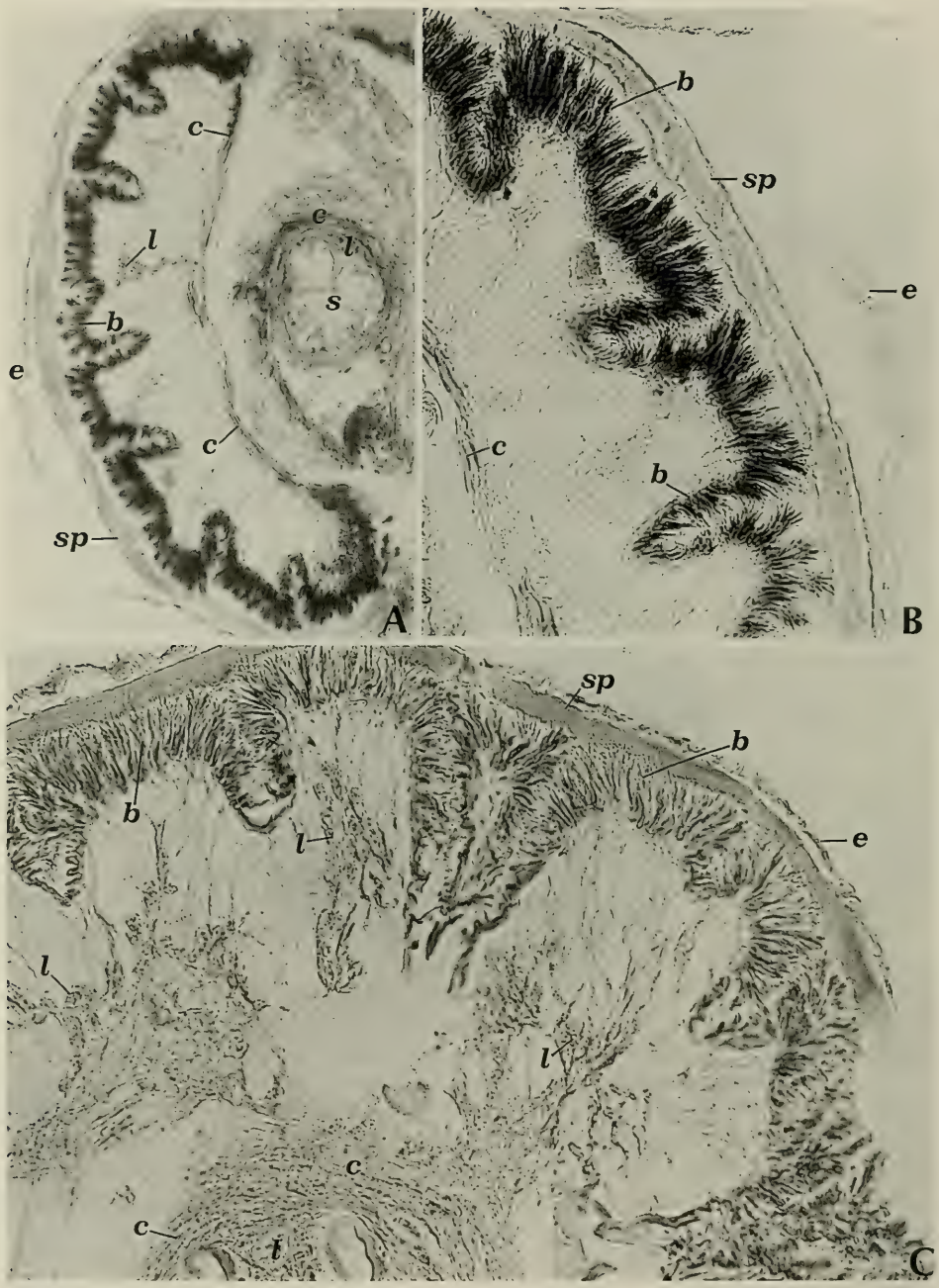


Fig. 347. *Cephalotes clypeatus* (FABRICIUS), proventriculus. A: longitudinal section (Azan). B: the same as A but at larger magnification (Azan). C: transversal section (Alcian blue). Lettering: *b*, pollen filtering bristles; *c*, circular muscles; *e*, epidermis; *l*, longitudinal muscles; *s*, stomodeal valve; *sp*, proventricular shield.

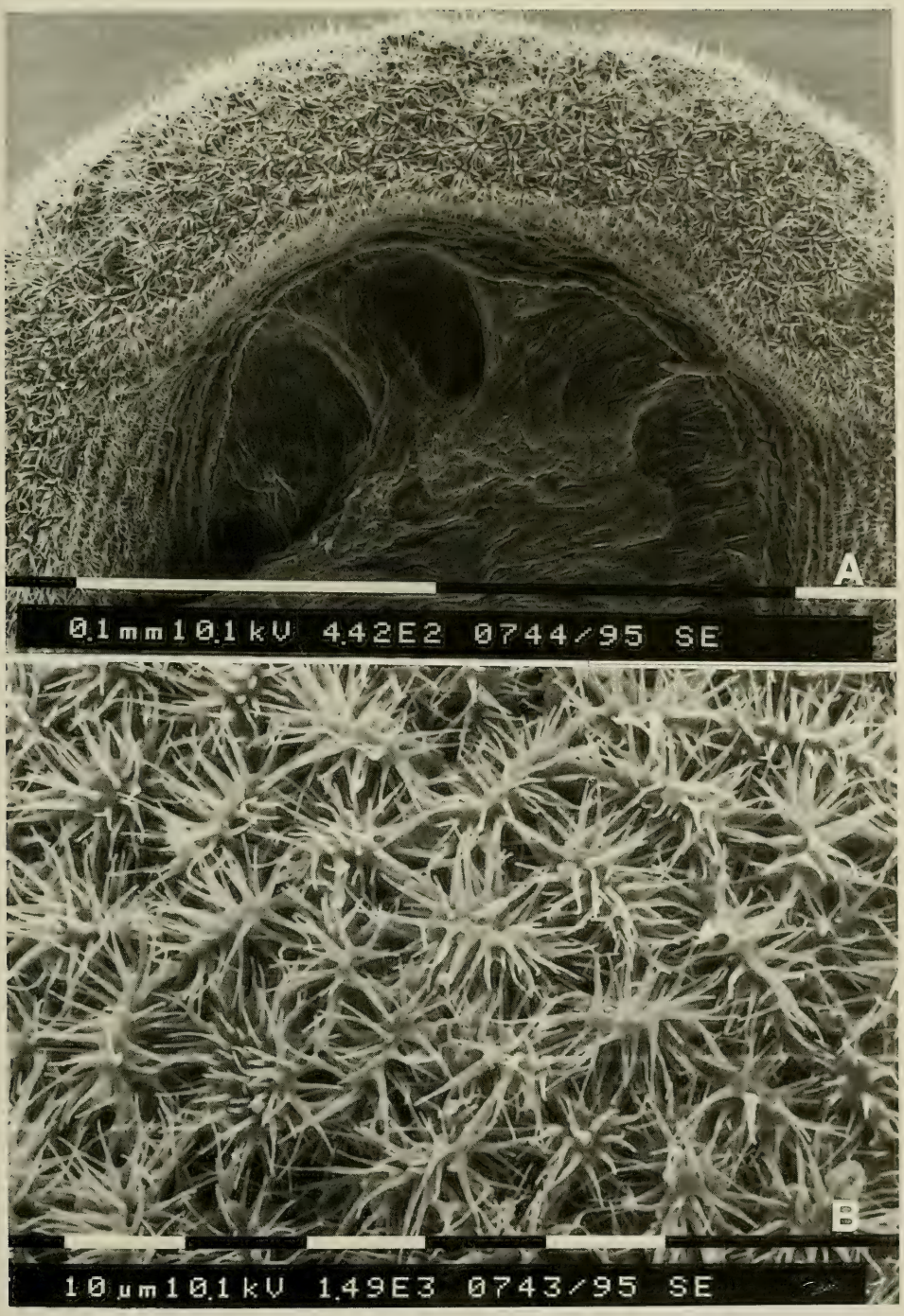


Fig. 348. *Cephalotes auricomus* (WHEELER), SEM micrographs of the posterior border of the proventricular bulb after remotion of the proventricular shield. A: maximum caudal extension of the pollen filtering bristles. B: details of the bristles.

perceivable in dorsal view only as a doubling or a thickening of the perimeter of the bulb (Figs. 346, A, B). We called this framework the proventricular shield (BARONI URBANI & DE ANDRADE, 1997): it completely embraces the umbrella dorsally and folds under it in part.

The *Cephalotes* proventriculus appears to be a powerful mechanical pump and filter, morphologically much more sophisticated than that of the honey-bee which is considered to be by far the most efficient known to date (BAILEY, 1954). The bulb of the proventriculus invaginates deeply into the crop and its surface appears divided into several irregular septa (Fig. 346).

Histological sections of the bulb (Fig. 347) reveal an important set of circular and longitudinal muscles around the stomodeal valve and within the septa. The septal muscles operate in a large, empty haemocoel in order to permit a strong pumping action. The bristles, of cuticular origin, exert the pollen filtering action by moving against the proventricular shield. SEM examination of the septal surface shows the dense covering by short, thick bristles which confer the filtering action (Fig. 348).

6.3.3. Origin and significance of the infrabuccal pellets

Dissection of freshly killed *C. pusillus* workers to which *Corylus* flowers had been offered allowed the regular presence of pollen grains in the crop to be ascertained. The function of the proventriculus is that of separating the grains from the liquid food thus storing the pollen grains in the crop preventing them from being passed into the ventriculus. Pollen, once in the crop, can be either digested, or stored. The digestion may occur via the saliva or via regurgitation of midgut enzymes. This appears to represent the first instance of pollen digestion in the fore gut among insects. Bees and other pollen eating Hymenoptera[1] – because of the lack of morpho-

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[1] Pollen feeding by *Cephalotes* received little attention by subsequent authors after it had been described by CREIGHTON (1963, 1967) and by CREIGHTON & NUTTING (1965). The few references to this behaviour we have been able to find in the literature stress that, if confirmed, the case is likely to be unique among ants.

As a matter of fact, the ant literature contains direct evidence for pollen ingestion and circumstantial evidence for pollen chewing and filtering by another group of ants: the Pseudomyrmecinae. WHEELER & BAILEY (1920) have been able to analyse the contents of the food pellets of the larvae of 24 nominal taxa belonging to this subfamily. They report the presence of pollen in the pellets of 15 species. For another one (*Pseudomyrmex flavidula* var. *delicatula*) the presence of pollen is not explicitly listed among the contents of the pellet but pollen is clearly visible in the relevant photograph (Plate II, Fig. 15).

In the same paper WHEELER & BAILEY (l. c.) describe a new structure present in the oral cavity of all larvae of this subfamily and – to a different extent – in members of other subfamilies as well. The structure described in this paper and in another contemporary paper by WHEELER (1920), is called t r o p h o r h i n i u m (literally feeding nose). It consists of two opposable surfaces within the mouth bearing rows of spinules limited on the postero-lateral edges by prominent sets of longer setae. Its function was supposed to be that of „triturating particles of food and sifting or straining out the coarser and harder pieces".

WHEELER (1920) describes and discusses at some length the morphology of the proventriculus of the Pseudomyrmecinae and concludes: „I find, however, that the proventriculus of all four genera of the Pseudomyrminae [sic] is much more specialised [than that of the Myrmicinae], being anteriorly developed as an apple- or quince-shaped ball, covered with longitudinal and circular muscles and with four distinct, connate sepals, bluntly rounded and finely hairy at their tips..."

All this seems to be consistent with pollen eating by the Pseudomyrmecinae and with a comparable morphological specialisation of their digestive tract for this function.

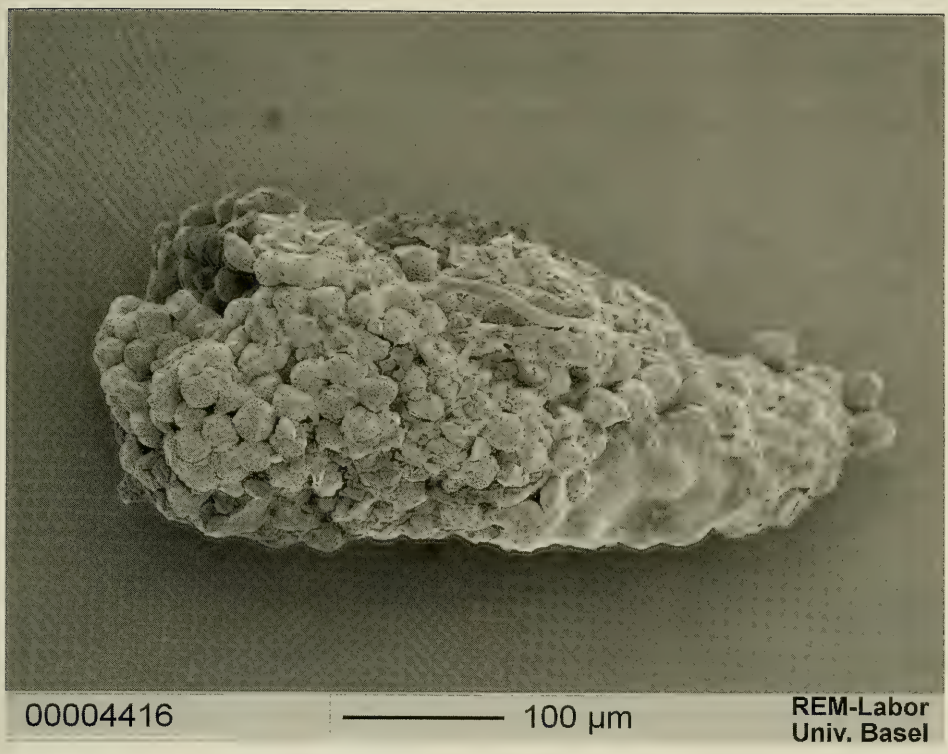


Fig. 349. *Cephalotes clypeatus* (FABRICIUS) pellet rejected outside the nest and consisting essentially of digested grains of pollen of *Hedera helix*.

logically specialised proventriculi – accumulate the pollen either in the gut or directly in the ventriculus with digestion occurring via diffusion of fluid through the peritrophic membrane such that the pollen grains pass through the whole intestine (BAILEY, 1954).

WHEELER & BAILEY (1920) described for the first time the presence of "infrabuccal pellets" among Cephalotini. WILSON (1976) arguing that the production of pellets, thus far, had been reported only among arboreal ants, suggested that such pellets are "a device used primarily for the conservation of water". On the other hand, regurgitation of infrabuccal pellets was not observed in *C. atratus* by CORN (1976) who explained the discrepancy by the fact that *C. atratus* nests on large living trees where water should not be a problem. We observed, however, the production of pellets in a laboratory colony of *C. atratus*.

As a matter of fact, there was no clear evidence suggesting that the cephalotine pellets should have been different from the "boulettes de nettoyage" described for terrestrial ants by JANET (1895, 1897). Subsequently, "infrabuccal pellets" were also reported from terrestrial ant genera like *Acromyrmex* (FEBVAY & KERMARREC, 1981) and *Solenopsis* (GLANCEY et al., 1981) thus further weakening the arboreal adaptation hypothesis.

WILSON (l. c.) observed *C. varians* workers offering pellets to larvae and re-con-

suming their own pellets. These observations are confirmed by COLE (1980) who, re-studying the same species, adds that infrabuccal pellets can also be passed from worker to worker. WHEELER (1984), while studying *Procryptocerus scabriusculus*, observed pellets frequently but these were regularly thrown out of the nest and never offered to other nestmates.

We systematically observed great numbers of rejected pellets on the floor of the arenas of the nests of all the species we kept in the laboratory (*angustus*, *atratus*, *borgmeieri*, *clypeatus*, *pallidoides*, *pusillus*, *targionii*). We explain the higher frequencies of pellets by the fact that we fed our ants regularly, though not exclusively, with pollen. These pellets appeared to be made out of different minute particles of solid materials among which pollen grains were often recognisable and represented the main component (Fig. 349).

Assuming the functional morphology of the cephalotine proventriculus as we described it under 6.3.2 as being correct, it is very probable that the pellets regurgitated outside the nest are the product of its filtering action. The nutrient-rich internal part of the pollen is probably digested through the pores of the micropylar membrane. The remaining indigestible food particles, are subsequently expelled in form of pellets. This hypothesis is consistent with the following known aspects of *Cephalotes* biology:

1. Pollen transport into the nest.
2. Highly specialised filtering morphology of the proventriculus.
3. Absence of cellulolytic bacteria for digesting the pollen shell.
4. Transmission of pellets to larvae and adult nestmates.
5. Regurgitation outside the nest of "used" pellets.
6. Absence of pollen in the mid- and hindgut of several species.

This explanation does not contradict previous descriptions of pellets being offered to, and accepted from, other nestmates, if one assumes that the pellets in question may contain still undigested or only partly digested pollen.

6.4. Caste systems, morphology and functions

One of the peculiarities of *Cephalotes* readily observable among some of its species, is the presence of a very odd neuter caste (the soldiers) characterised by a very large saucer-shaped head. Other species exhibit a comparable two caste system, but there the head of the soldiers bears no disc-like structure and is simply broader and rounded posteriorly. *C. atratus* is apparently characterised by a small difference in size from a basically unique worker morphology. Finally, for the poorly known Hispaniolan endemics representing the former subgenus *Hypocryptocerus*, soldiers have never been collected and there is supposed to be only one, monomorphic, worker caste, though the small number of individuals available in the collections hardly suffices for such conclusion. We can now confirm what had been previously supposed by many, i. e. the absence of soldiers in these ants after one of us (MLDA) collected a complete colony of *C. auricomus* with queen, males and winged gynes in the Dominican Republic.

Cephalotes soldiers, when present, bear mandibles proportionally much more reduced than those of most other ants to which the term soldier has been applied. Additionally, the soldiers of several (but not all) *Cephalotes* species exhibit a cephalic morphology nearly identical to that of reproductive females. This caste polymorphism is different from that known for other ant species but very similar to

that of some phylogenetically distant *Camponotus* species with which they share similar ecological requirements. However, not all *Cephalotes* species appear to possess a highly differentiated soldier caste with disc-shaped head. The presence or absence of soldiers had been used, in the past, as a character to separate some subgenera and genera now included in *Cephalotes*. KEMPF (1951), for instance, distinguished the "genera" *Zacryptocerus* and *Hypocryptocerus* on the basis of possessing or not possessing a two caste system. As we already said, most, but not all, the species with a single, monomorphic neuter caste belong to the former subgenus *Hypocryptocerus* (= our *hamulus* clade) and are endemic to the island of Hispaniola.

6.4.1. Morphometric characterisation of the neuter castes

As previously observed by BARONI URBANI (1974), under the heading of polymorphism the ant literature contains descriptions of rather different phenomena, i. e. sex dimorphism (WHEELER, 1907 a: 50; ESCHERICH, 1917: 46; WILSON, 1971: 136; HÖLLDOBLER & WILSON, 1992: 301), differentiation of the neuter caste(s) (several references), and intra- and inter-caste variation (see e.g. WILSON, 1953).

Sex dimorphism has received little attention by modern students. Within *Cephalotes* the differences between males and gynes of the same species are rather constant and not too dissimilar from that known from other myrmicines. We shall therefore not deal with this phenomenon.

The modern study of caste variation was initiated by WILSON (1953) using a biometric approach already employed by HUXLEY (1927). This approach, in spite of the invalid assumption associating the presence of allometry with the origin of a novel caste within workers, stimulated several papers by other students and we regard it as one of the most practical methods for describing iso- or allometric growth within each caste. Despite several similar studies in the literature, we would like to emphasise an important point stressed by VAN BOVEN (1970) which received very little attention among subsequent students, i. e. that by comparing different pairs of body parts one may obtain substantially different results. Most available biometric descriptions of ants' polymorphism are undertaken using bivariate scattergram plots, with or without logarithmic axes. Allometry is detected by visual examination of the shape of the best fitted linear regression line. BARONI URBANI (1976) recommended the use of polynomial regressions of increasing degree since they lead to a higher degree of fit with the original measures when multiphasic allometry is present. Polynomial regressions, however, give better results when different castes are analysed together, as has occurred until now, instead of separately, as will be done in the present study. This kind of biometric approach is unlikely to account for dramatic intercaste morphological changes such as between the gynes and the workers of most ant species, and between the gynes and the soldiers as they are observed in some species of *Cephalotes*. Differentiation of neuter castes and, in part, of soldiers, has been studied carefully in a few representative ant species, essentially from the point of view of the exogenous and endogenous factors regulating the postembryonic development (see e. g. reviews by BRIAN, 1979, BUSCHINGER, 1990, and BARONI URBANI & PASSERA, 1996). The morphogenetic changes due to caste formation have been tentatively analysed by BARONI URBANI (1974) in some species of *Camponotus* by means of transformation grids derived from those of D'ARCY

THOMPSON (1917). FRANKS & NORRIS (1987) used the same method on a sample of species belonging to different genera to describe worker and worker-soldier transformations. No quantitative analyses have been conducted on the intercaste polymorphism of the Cephalotini where the phenomenon reaches its maximum known extent. Caste polymorphism is one of the most astonishing traits of *Cephalotes* and it will be analysed here at some length using biometric analyses and D'ARCY THOMPSON's cartesian transformation grids as described in the methods chapter.

The sole available descriptions of intra-caste polymorphism in *Cephalotes* to date are those given by CORN (1976, 1980) for the worker of *C. atratus*; and those of BARONI URBANI & PASSERA (1996) for the gyne, soldier and worker of *C. angustus*. In these studies pairs of body measures are investigated traditionally by means of scattergrams and frequency distributions (for *atratus* only). These results, however, are far from being representative for the whole genus since, within *Cephalotes*, different species exhibit different caste systems encompassing most of the diversity known for the ants as a whole.

In the present analysis we shall deal with a limited number of species intuitively selected as being representative of the major evolutionary caste trends we recognise within *Cephalotes*. The exact strategy and methodological details of the procedure employed in this paper are given in chapters 4.4.1 and 4.4.2.

At least the following three intuitive types of caste polymorphism can be easily recognised:

6.4.1.1. Single caste system

The presence of only one neuter caste is probably universal among all the members of the endemic Hispaniolan *hamulus* clade. This had been already supposed in the literature and has been confirmed by our first collection of a complete nest of *C. auricomus* in the Dominican Republic. To describe caste differences biometrically we measured the maximum pronotal width and the hind tibia length of all gynes of this colony, including the single queen (i. e. 24 gynes), and of a random sample of 109 workers as described in the methods chapter.

Examination of the frequency distributions of both measurements reveals a great degree of overlap between workers and gynes in pronotal width (Fig. 350) and even greater for the hind tibia length (Fig. 351). As one might expect, the individual frequency distributions differ somewhat from the norm and from caste to caste. This can be described as follows:

	pronotal width		hind tibia length	
	skewness	kurtosis	skewness	kurtosis
gynes	–0.113	–0.235	–0.005	–0.959
workers	0.308	0.714	–0.811	2.767

We are inclined not to attribute excessive importance to these deviations from normality as they may be partly dependant on the size of our sample.

Within both workers and gynes, individual variation appears to be of larger magnitude than covariation of the two body parts.

The best explanatory regression model for our two variables based on comparison of the adjusted R^2 statistics gives the following results:

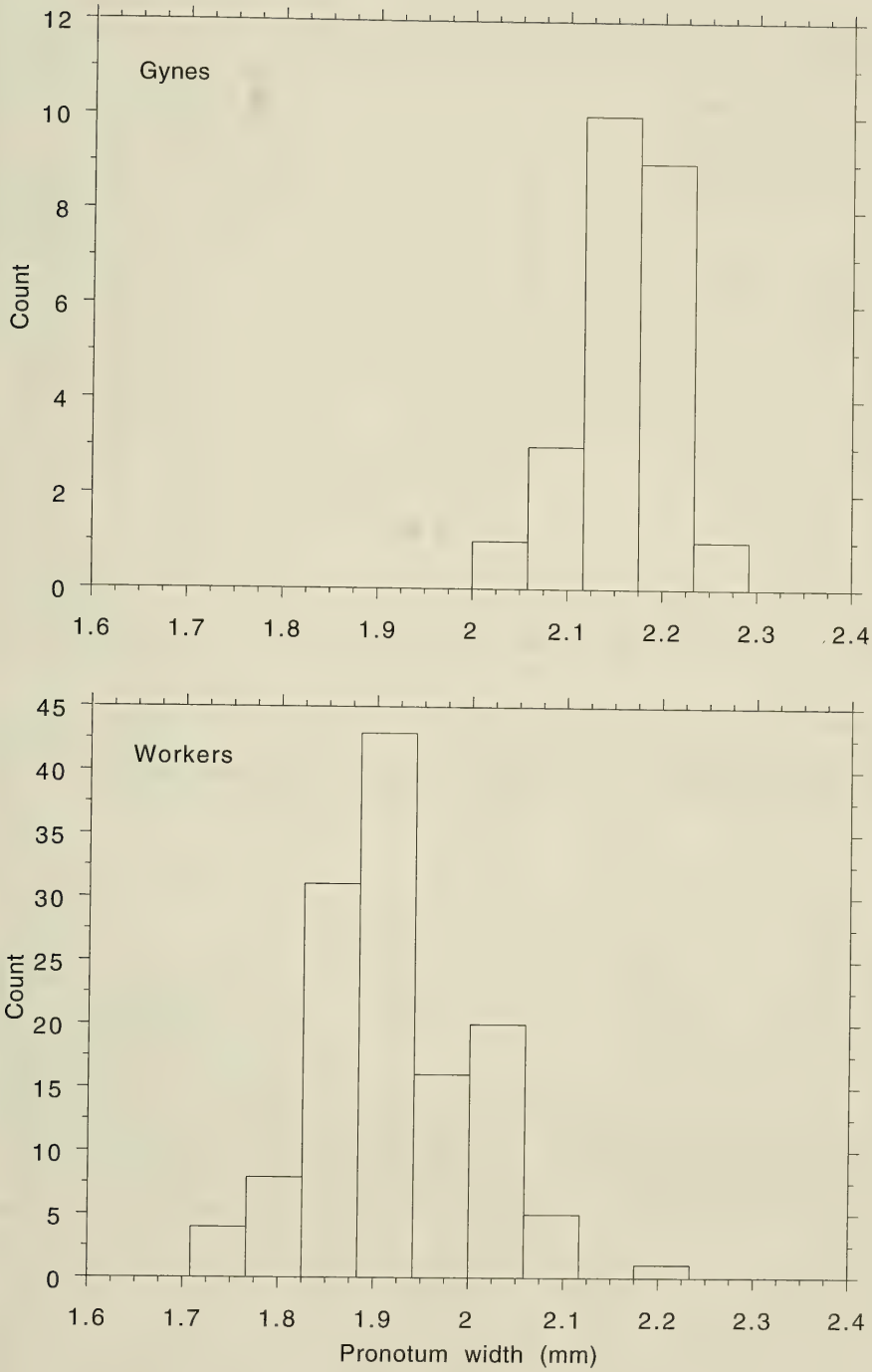


Fig. 350. *Cephalotes auricomus* (WHEELER). Frequency distributions of the maximum pronotal width of a sample of the two female castes within a single nest from the Dominican Republic.

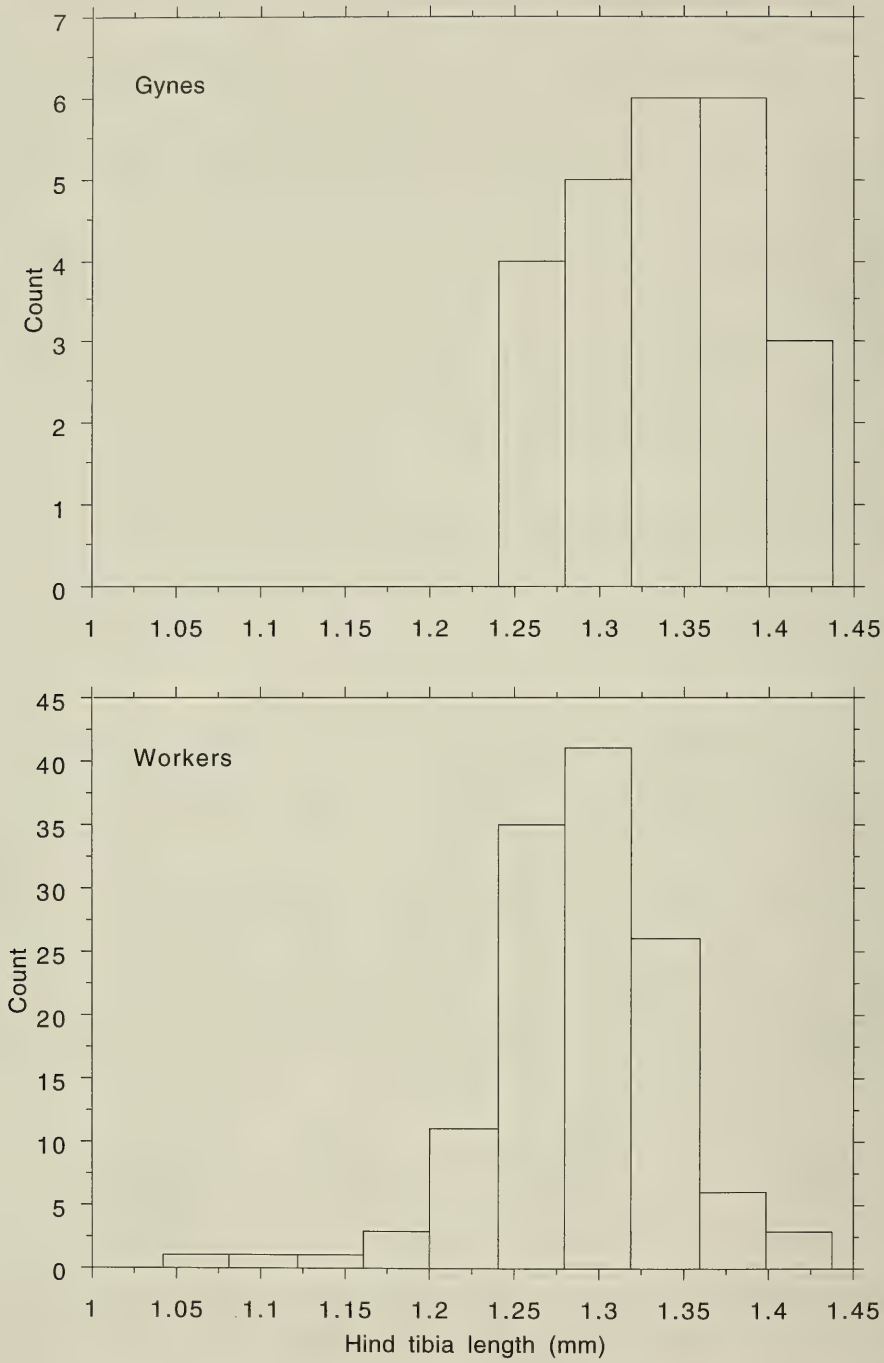


Fig. 351. *Cephalotes auricomus* (WHEELER). Frequency distributions of the hind tibia length of a sample of the two female castes within a single nest from the Dominican Republic.

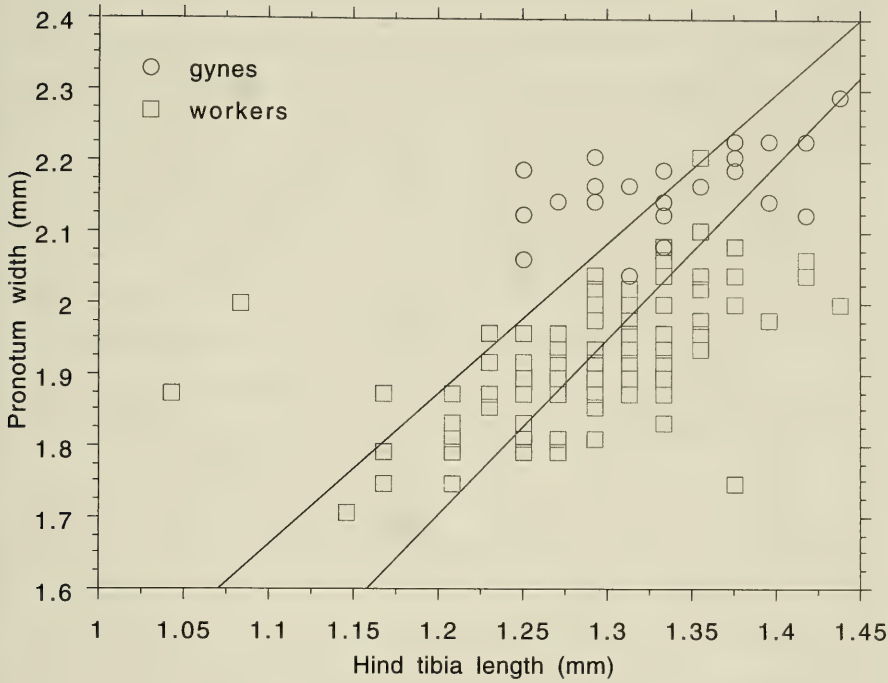


Fig. 352. *Cephalotes auricomus* (WHEELER). Scattergram and relative regression lines of the maximum pronotal width and hind tibia length of a sample of females from a single nest from the Dominican Republic divided by caste.

Regression	Workers	Gynes
Simple, rough data	0.305	0.225
Simple, log-transformed data	0.294	0.037
Polynomial, degree 2	0.302	0.251
Polynomial, degree 3	0.299	0.222

Simple regression, therefore, accounts better for the relative growth of worker pronotal width and hind tibia length. For gynes, the simple regression among the same body parts is bettered only by a second degree polynomial model but, since the latter involves less than a 3% improvement in terms of R^2 statistics, it has not been retained as being clearly superior to the simple regression.

Fig. 352 is a scattergram of the values of both body parts among workers and gynes. The regression equations with, in square brackets, twice the Standard Error are for gynes:

Pronotum width = 1.434 [± 0.526] + 0.545 [± 0.394] x (Hind tibia length)

and, for workers:

Pronotum width = 0.935 [± 0.262] + 0.765 [± 0.202] x (Hind tibia length).

No statistically significant difference can be demonstrated between the regression equations of gynes and of workers.

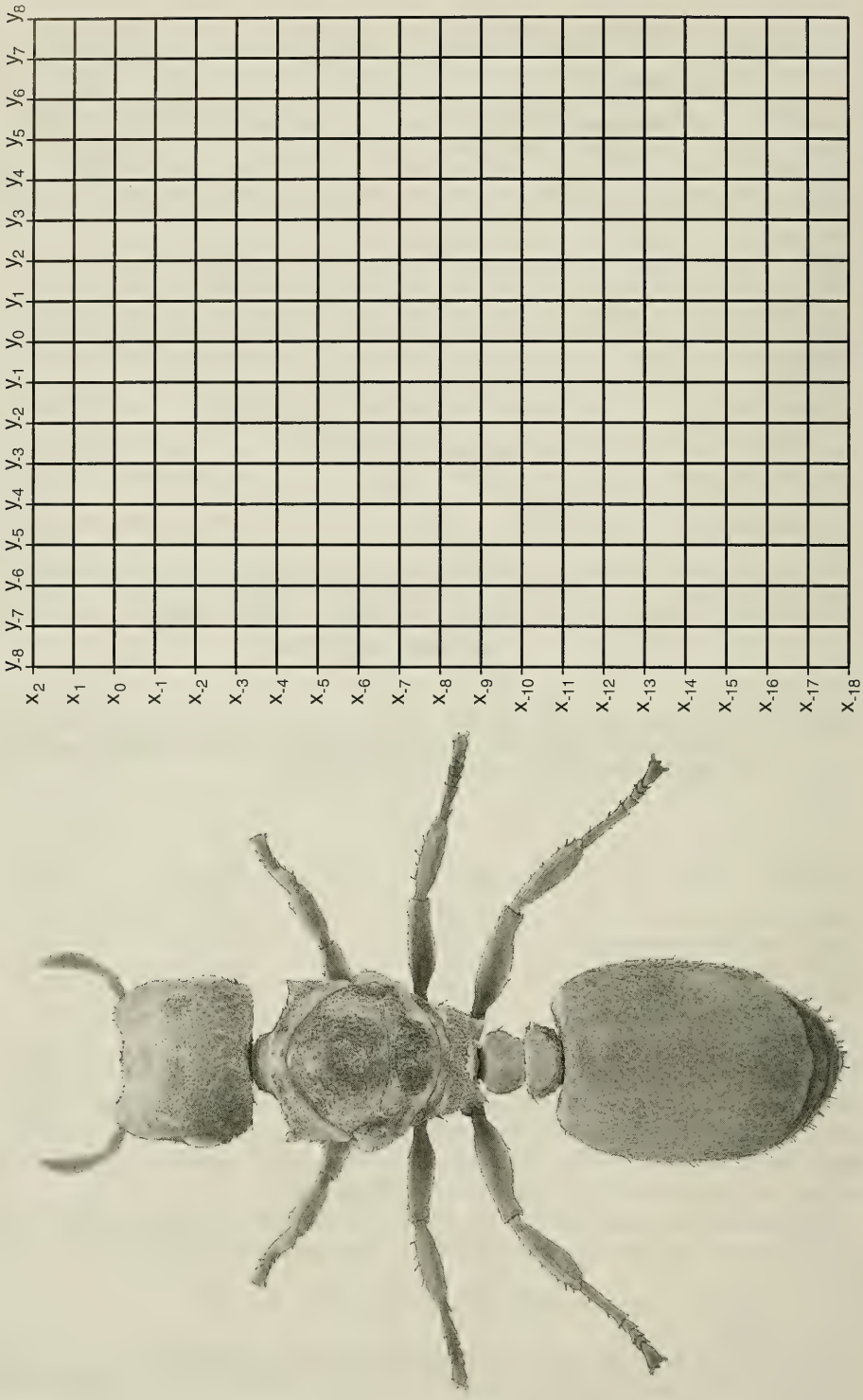


Fig. 353. *Cephalotes auricomus* (WHEELER), gyne and the relative untransformed grid.

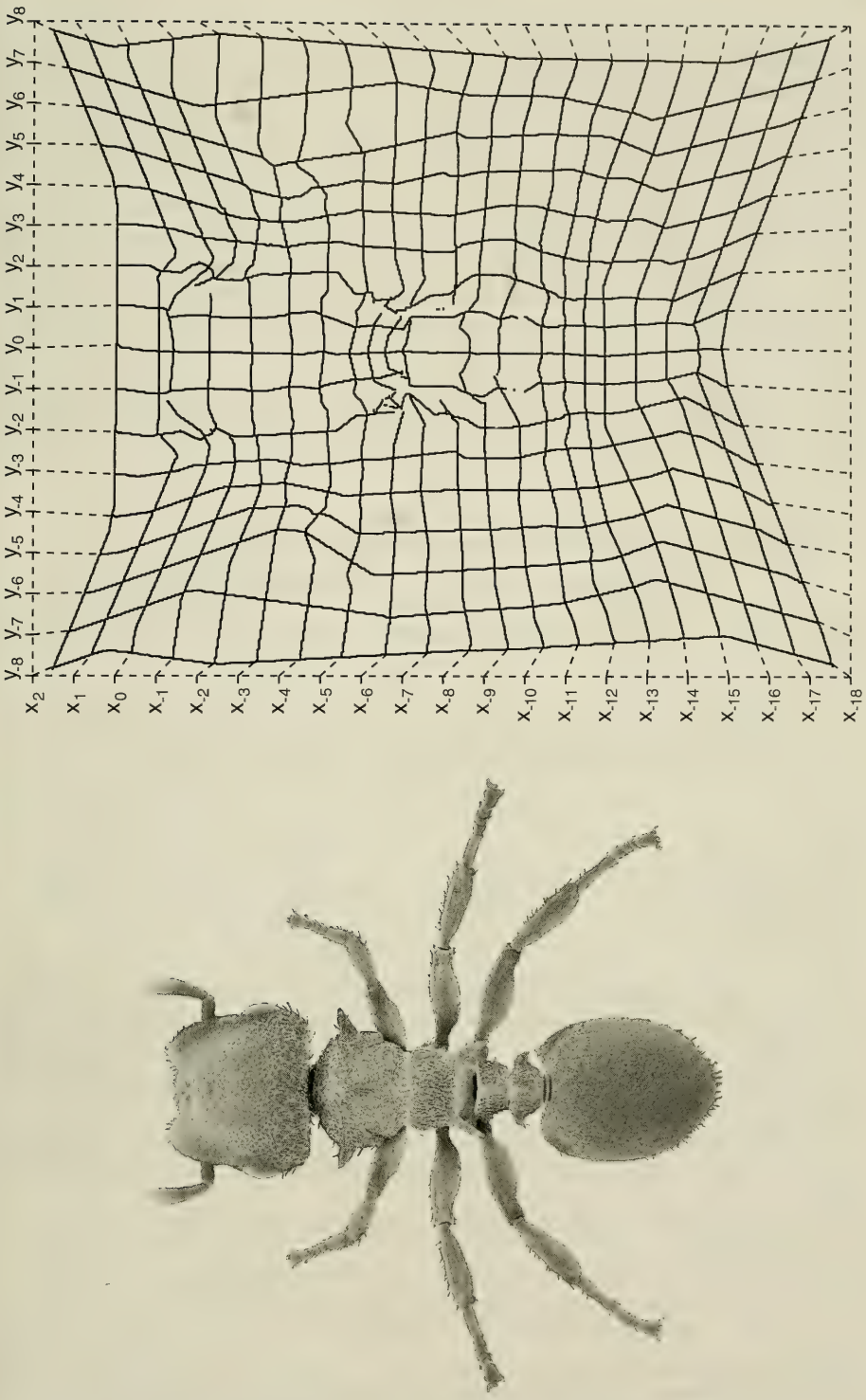


Fig. 354. *Cephalotes auricomus* (WHEELER), worker and worker-transformed gyne grid.

Figs. 353 and 354 show the non-transformed, geometrically regular gyne grid and the worker-transformed grid relative to this species. The two castes are not very dissimilar either in size or in proportions and the greater changes – as one would expect – are expressed by the abscissas x_{-6} - x_{-8}, i. e. by the coordinates relative to the meso- and metathoracic sclerites. In this sense, the gyne-worker caste differentiation of this species is among the least impressive for the whole subfamily Myrmicinae.

C. atratus is one of the few species outside the *hamulus* clade with a similar caste system. Other species of the *atratus* clade, when known on large series, regularly show a morphologically differentiated soldier caste. We cannot exclude, however, that other species of the same clade known only from a few workers (e. g. *oculatus*, *placidus*), may also exhibit a one caste system. CORN (1980), for *atratus*, describes a weakly bimodal frequency distribution of head widths and allometric growth in a log-log plot of the width of prothoracic spines (equivalent to our maximum pronotal width) against head width. The material available to us shows a complete overlap of the two standard measurements we took among gynes and workers (Figs. 355 & 356).

All frequency distributions differ from normality as follows:

	pronotal width		hind tibia length	
	skewness	kurtosis	skewness	kurtosis
gynes	–1.160	0.627	–0.251	–0.604
workers	0.442	–0.446	0.071	–0.645

The best explanatory regression model for our pair of variables based on comparison of the adjusted R^2 statistics gives the following results:

Regression	Worker	Gyne
Simple, rough data	0.851	0.565
Simple, log transformed data	0.855	0.577
Polynomial, degree 2	0.869	0.592
Polynomial, degree 3	0.867	0.553

Hence simple regression accounts reasonably well for the relative growth of worker pronotal width and hind tibia length. In fact, a second degree polynomial regression gives the best results for both gynes and workers but the model has been not adopted since it involves a less than 3% improvement over the simple regression model in terms of R^2 statistics.

Fig. 357 is a scattergram of the values of both body parts among workers and gynes. The regression equations with 2x Standard Error for each coefficient are for gynes:

Pronotum width = –0.247 [± 0.860] + 1.469 [± 0.398] x (Hind tibia length)

and, for workers:

Pronotum width = –0.695 [± 0.224] + 1.459 [± 0.055] x (Hind tibia length).

Notice the difference in the intercept and the practically identical slopes between the two curves. The difference, however, cannot be demonstrated to be statistically significant.

The main biometric difference between gynes and workers for both species exhibiting this type of caste system appears to be in size rather than in allometry and

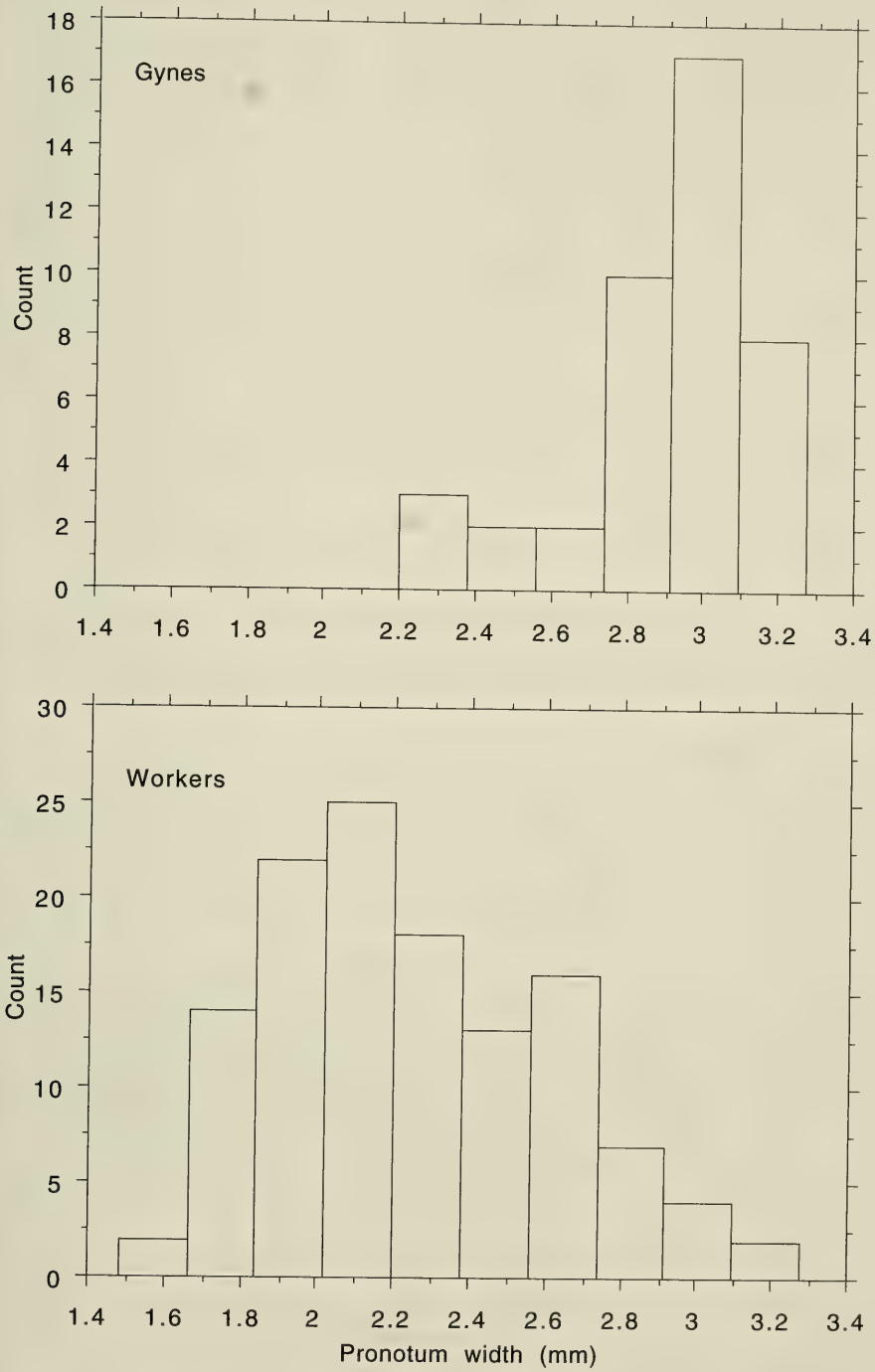


Fig. 355. *Cephalotes atratus* (LINNAEUS). Frequency distributions of the maximum pronotal width of a sample of the two female castes. The workers originate from a single nest from Lins (S. Paulo) and the gynes from different Brazilian localities.

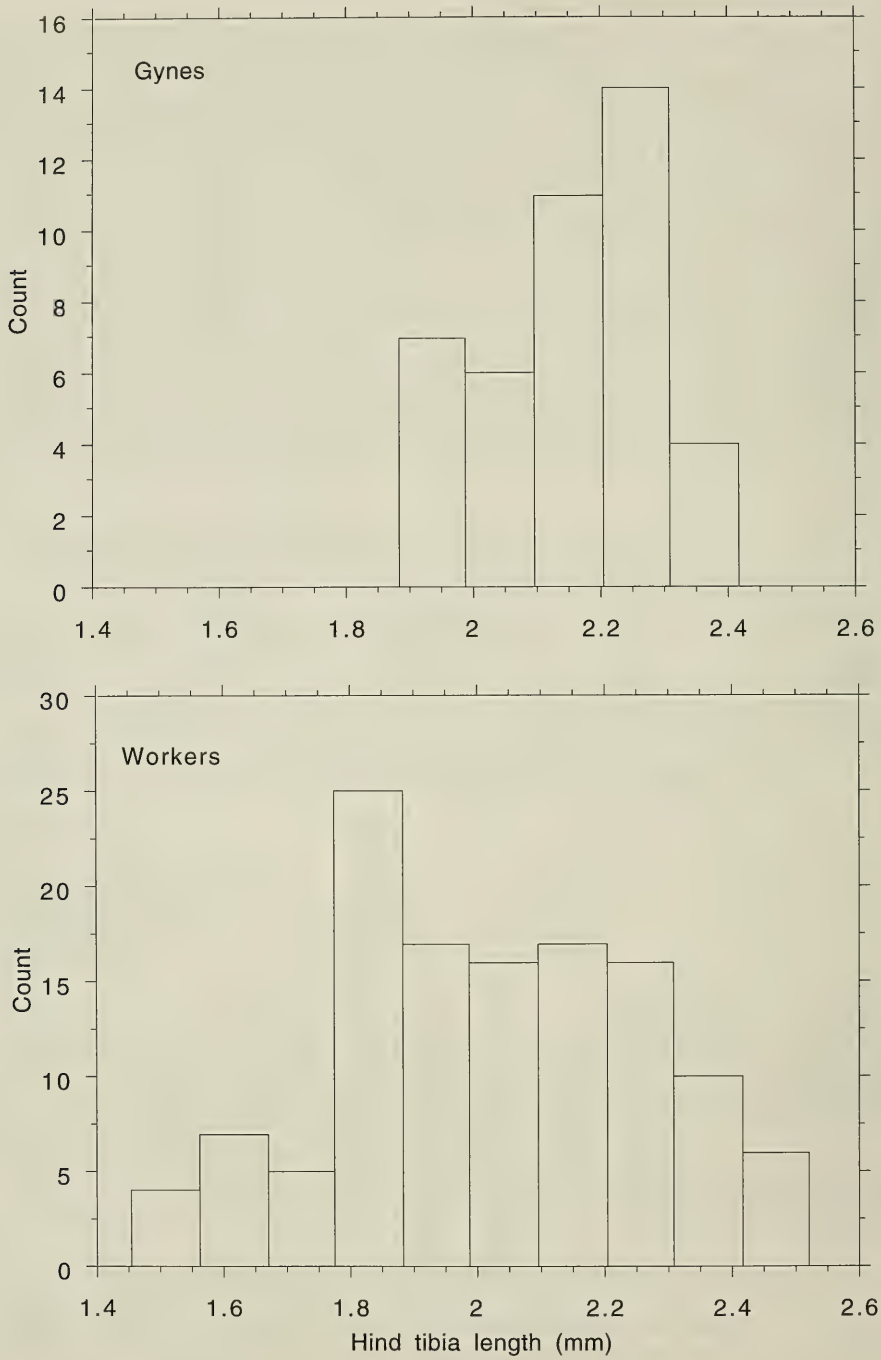


Fig. 356. *Cephalotes atratus* (LINNAEUS). Frequency distributions of the hind tibia length of a sample of the two female castes. The workers originate from a single nest from Lins (S. Paulo) and the gynes from different Brazilian localities.

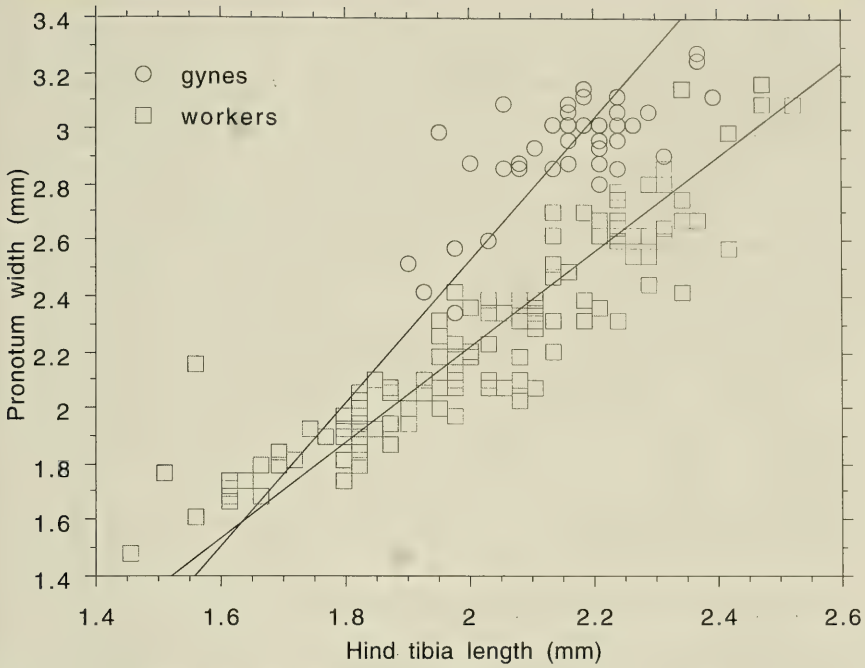


Fig. 357. *Cephalotes atratus* (LINNAEUS). Scattergram and relative regression lines of the maximum pronotal width and hind tibia length of a sample of females from different Brazilian localities divided by caste.

this – as was to be expected – is much more evident in pronotal width than in tibia length. The size differences, however, remain modest and none of the body parts measured can be used as a criterion for caste discrimination since there are too many cases of inter-caste overlap. Neither the frequency distributions of these two body parts nor the best fitting regression line suggest the presence of morphologically separate subcastes.

The non-transformed gyne grid and two worker-transformed grids revealing the changes observable among major and minor workers of *C. atratus* are shown in Figs. 358, 359 and 360. The difference in size between gyne and workers appears to be relatively unimportant in this species – as it is in *auricomus* – and, if important, it essentially affects more the body than the appendages which are very similar in the two castes. A general reduction in worker body size – as compared with that of *auricomus* – is indicated by the much more concave shape of both x_0 and x_{-16}. The vertical coordinates subject to major change are the $y_{|2|}$, i. e. those expressing the growth of the vertexal, pronotal and propodeal spines. Transformation of the abscissae $x_{-6} - x_{-8}$ expresses the disappearance of the thoracal sclerites in a way analogous to that observed in *auricomus*. To these obvious transformations, one should add a remarkable shrinking of the fields between $x_{-2} - x_{-4}$, and $y_2 - y_{-2}$, and of those between $x_{-12} - x_{-17}$ and $y_2 - y_{-2}$, i. e. of those expressing the size of the head and of the gaster. This phenomenon is much more significant in *atratus* than in *auricomus*. Hence, the former is subject to much greater differentiation in workers than the latter. There seem to be no significant differences between major and minor workers.

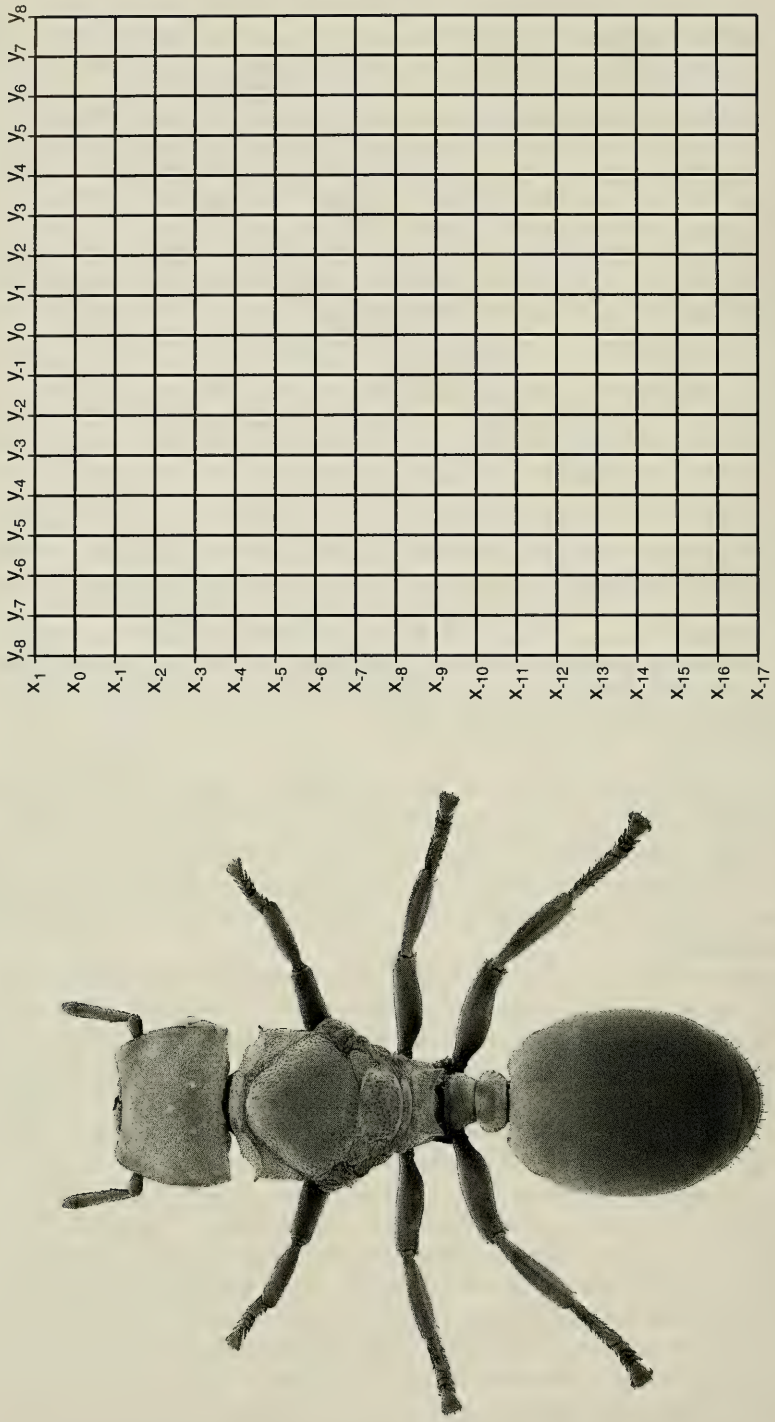


Fig. 358. *Cephalotes atratus* (LINNAEUS), gyne with the relative untransformed grid.

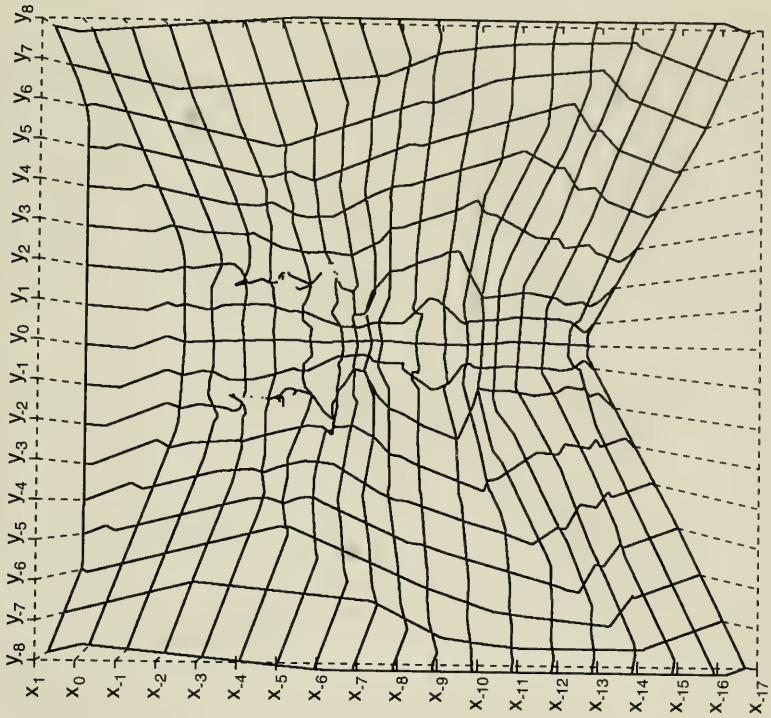


Fig. 359. *Cephalotes atratus* (LINNAEUS), major worker with the relative transformed gyne grid.

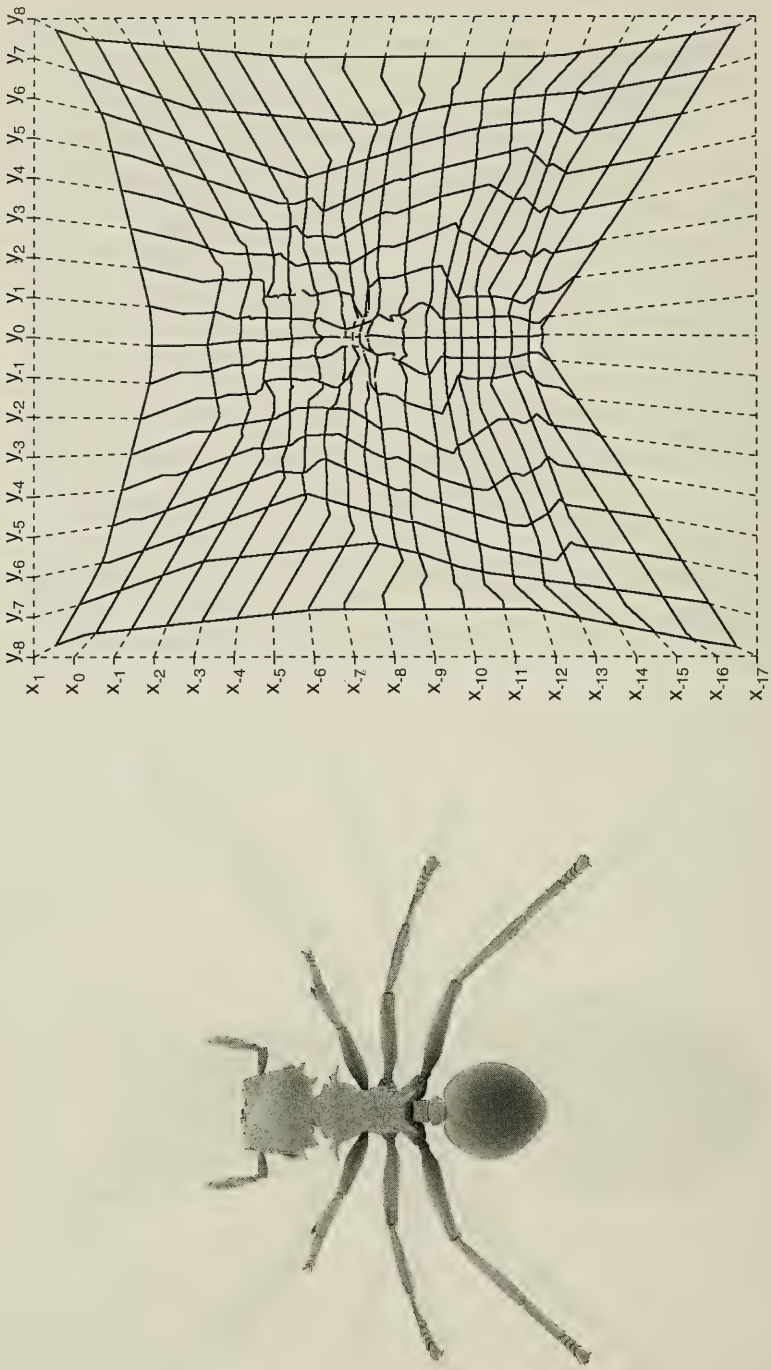


Fig. 360. *Cephalotes atratus* (LINNAEUS), minor worker with the relative transformed gyne grid.

6.4.1.2. Two-caste system with unspecialized soldiers

The remaining sufficiently well known members of the *atratus* clade (i. e. *alfaroi* and *serraticeps*), all the members of the *pusillus*, *complanatus* and *multispinosus* clades, and two out of three members of the *clypeatus* clade (*clypeatus* and *ustus*) evolved two discrete neuter castes, i. e. workers and soldiers as described below. Practically, individuals intermediate between workers and soldiers seldom exist and the great majority of the neuters of a nest can be unequivocally assigned either to the worker or to the soldier caste. Because of their discrete nature, members of each caste will be treated separately in our biometric analysis. Biometry, however, is not the best instrument to describe castes which may differ clearly from each other in morphology and often overlap in size (see e. g. the wide overlap in pronotal width and hind tibia length among workers, soldiers and gynes of *C. pusillus* in Figs. 361 & 362). It is unfortunate that KEMPF in most of his papers on Cephalotini appeared to differentiate soldiers from workers essentially by means of their size or by the presence or absence of the cephalic disk. In his papers, small individuals with a typical soldier morphology and large individuals with obvious worker morphology are often designated as "intermediate" forms between workers and soldiers. In the *depressus* clade where the soldiers are regularly present as a caste but have only a round posterior flattening of the head, KEMPF (1951: 218), after describing the soldier of *cristatus*, states that "the full-grown soldier appears to be very rare, since I have not seen any specimen of that caste, although a few workers examined were slightly intermediate...".

The soldiers are easily recognisable, apart from the often larger body size, based on an important set of morphological characters the most visible of which are probably:

1. Stouter, corpulent body structure.
2. Transverse pronotal carina (the possible exception, *manni*, has been already discussed in the introduction to the key to the soldiers, Chapter 5.8.2).
3. Convex, broader head.
4 Loss of vertexal lamellae (exceptions: *goeldii*, *notatus*, *frigidus*, *pallidicephalus*) and spines.
5. Presence or increase (if present in workers) of a pair of frontal teeth (in species without disc).
6. Cephalic disc.
7. Eyes largely concealed by the frontal carinae.
8. Reduction of mesosomal spines.
9. Reduction of the gastral expansions (when present in the worker).

Measurements of the maximum pronotal width (spines included) and of the hind tibia length of the Brazilian *C. pusillus* nest sub-sample of 145 workers, 40 soldiers and 61 gynes already mentioned in the material chapter gave clearly unimodal frequency distributions for both body parts, when separated by caste (Figs. 361, 362).

These figures show that there is little overlap between gynes and workers with respect to hind tibia length and no overlap at all with respect to pronotal width. The soldiers, however, occupy an intermediate position between gynes and workers and their minimum and maximum values overlap with both. In general, size separation is much clearer between castes than for species with only one caste. The relative deviations from normality of the frequency distributions of these body parts are as follows:

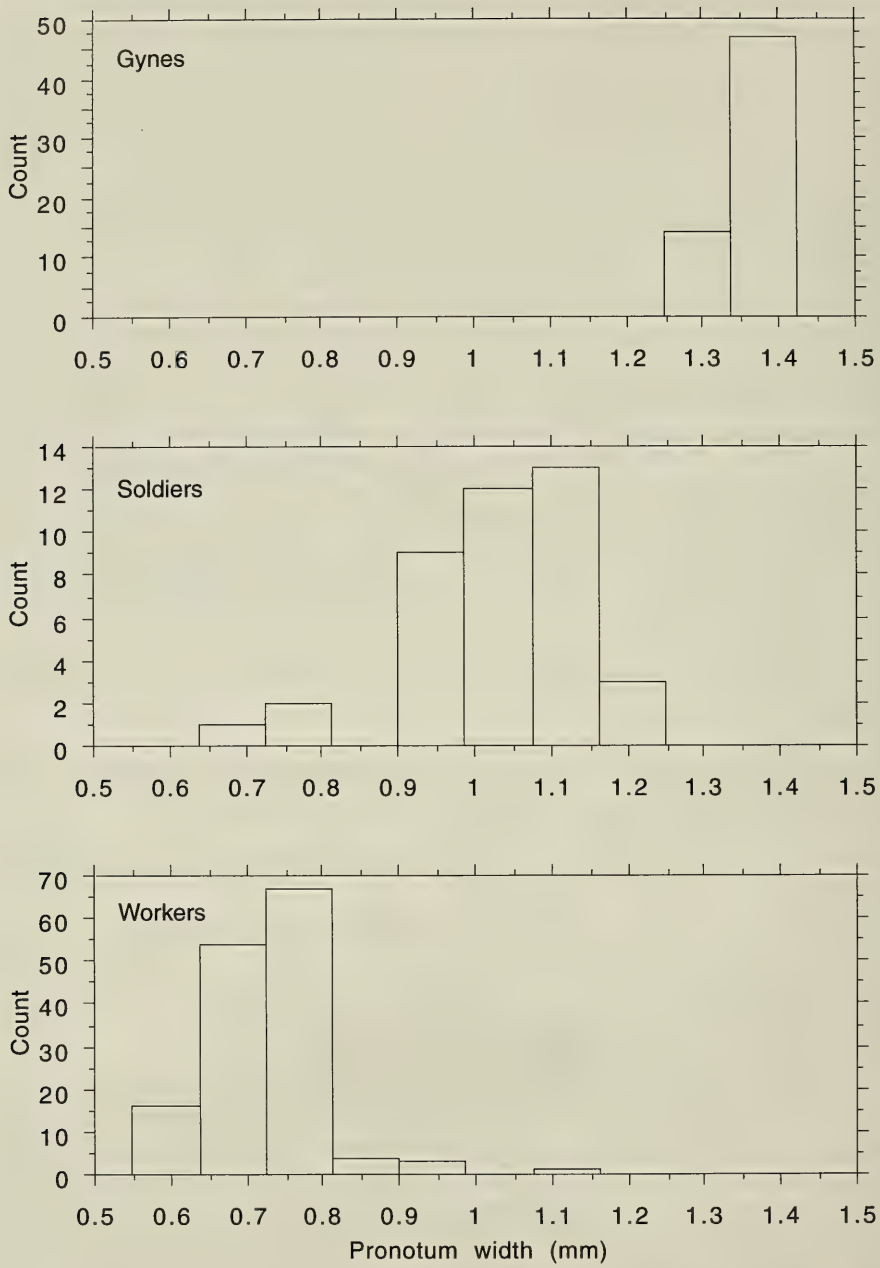


Fig. 361. *Cephalotes pusillus* (KLUG). Frequency distributions of the maximum pronotal width of a sample of the three female castes from a single colony from Botucatu (São Paulo).

Fig. 362. *Cephalotes pusillus* (KLUG). Frequency distributions of the hind tibia length of a sample of the three female castes from a single colony from Botucatu (São Paulo).

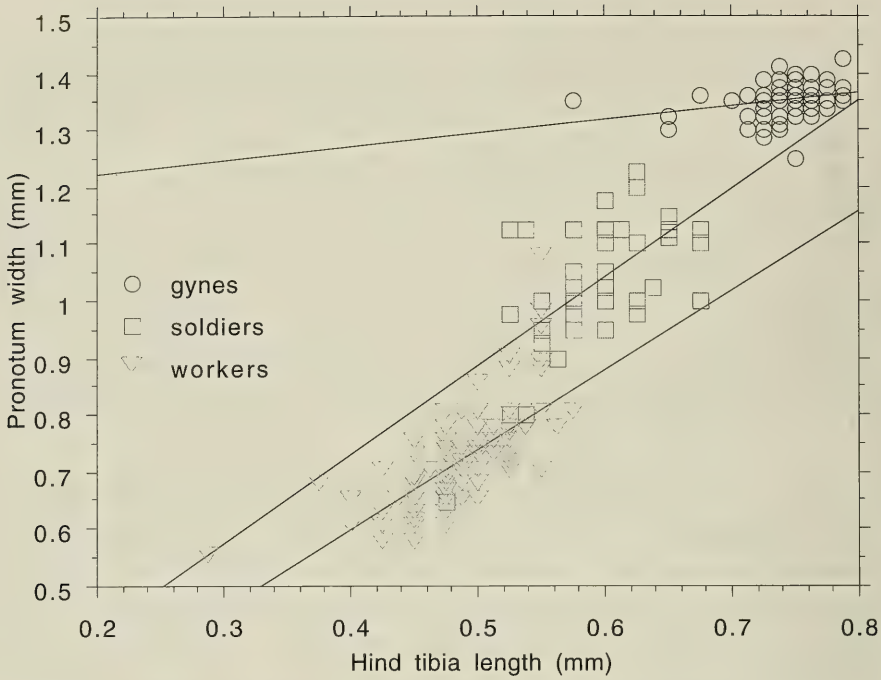


Fig. 363. *Cephalotes pusillus* (KLUG). Scattergram and relative regression lines of the maximum pronotal width and hind tibia length of a sample of females from a single nest from Botucatu (S. Paulo) divided by caste.

	pronotal width skewness	kurtosis	hind tibia length skewness	kurtosis
gynes	–0.515	1.060	–1.965	5.841
soldiers	–1.032	1.618	–0.221	–0.268
workers	1.212	4.078	–1.201	5.525

We do not attribute great biological significance to these deviations for the purpose of caste description.

Plotting the same pairs of measures together (Fig. 363) and testing the degree of fit by a set of models of increasing complexity gives the following adjusted R^2 values:

Regression	Gyne	Soldier	Worker
Simple, rough data	0.472	0.374	0.620
Simple, log transformed data	0.055	0.411	0.471
Polynomial, degree 2	0.058	0.380	0.531
Polynomial, degree 3	0.053	0.365	0.536

Simple regression accounts much better than the other models we tested for the variation observed among gynes and soldiers. A log-log transformation in terms of adjusted R^2 is slightly better (ca. 4%) but only for soldiers, representing an improvement below our arbitrary threshold of 5%.

The regression equations (figures in brackets are 2 x Standard Error) are for gynes:
Pronotum width = 1.177 [±0.156] + 0.236 [±0.212] x (Hind tibia length)
for soldiers:
Pronotum width = 0.107 [±0.376] + 1.556 [±0.632] x (Hind tibia length)
and, for workers:
Pronotum width = 0.041 [±0.120] + 1.393 [±0.244] x (Hind tibia length).

Our regression curves show substantially similar patterns for workers and soldiers, and both are considerably different from the regression line of gynes. Statistically, however, workers differ from both gynes and soldiers with respect to the intercept of the regression line.

Hence *C. pusillus* castes appear as discrete sets of individuals characterised primarily by morphology; biometrically, each caste is better defined by its distinctive allometric equation rather than by the different phases of a unique equation describing the polymorphism of all individuals. This suggests once more that the factors controlling caste determination in *C. pusillus* should be more complex than simple quantitative trophic differences during individual ontogenesis.

The *pusillus* transformation grids of Figs. 364, 365 and 366 must be dealt with separately. First, the soldier transformation grid (Fig. 365) shows a displacement of the cephalic fields $y_3 - y_{-3}$, and $x_0 - x_{-4}$, without remarkable modification of their size. This situation recalls the one observed among workers of *auricomus* and, less so, of *atratus*. On the other hand, the gastral fields of the *pusillus* soldier lying between $y_2 - y_{-2}$ and between $x_{-9} - x_{-15}$ are subject to a lesser shrinking as compared with the one observed in the workers of the previous species. The most remarkable and unexpected soldier character, probably, is an increasing of the size of the fields between $x_{-8} - x_{-9}$ and $y_2 - y_{-2}$ corresponding to the propodeal area.

The *pusillus* worker transformation grid stresses the dramatic size reduction that this caste has undergone. Compared with the soldier the main difference is the size reduction in the cephalic and gastral fields between $y_3 - y_{-3}$, and $x_0 - x_{-4}$, $y_2 - y_{-2}$ and between $y_2 - y_{-2}$ and $x_{-9} - x_{-15}$. A worker character, absent in the previously examined species, appears for the first time in *pusillus* and is also revealed by the transformed grid: the flattened vertexal angles.

We thought it interesting at this point to analyse another species in the same way which, *a priori*, may be expected to reveal additional information, namely *C. borgmeieri* (Figs. 367, 368, 369). This species in fact makes transition to the most specialised *Cephalotes* species for having soldiers with slightly differentiate cephalic disc on the posterior part of the head only.

The gynes and workers of this species are roughly similar to those of *pusillus*, but the soldiers show an incipient formation of the cephalic disc. This incipient disc is easily detectable under a microscope as a broadening and dorsal flattening of the cephalic capsule. And the *borgmeieri* soldier transformed grid shows an increase in size of ca. 15 % of the cephalic fields $y_3 - y_{-3}$, and $x_0 - x_{-4}$ as compared with the corresponding gyne fields. The shape of the other coordinates seems not to differ in a significant way from what we have already said about the *pusillus* soldier.

The grid corresponding to the *borgmeieri* worker is also very similar to that drawn for the *pusillus* worker. The main difference between the two appears to lie in the lateral expansions of the pronotum and is reflected in the different shapes of the fields occurring between $y_2 - y_{-2}$, and $x_{-7} - x_{-8}$.

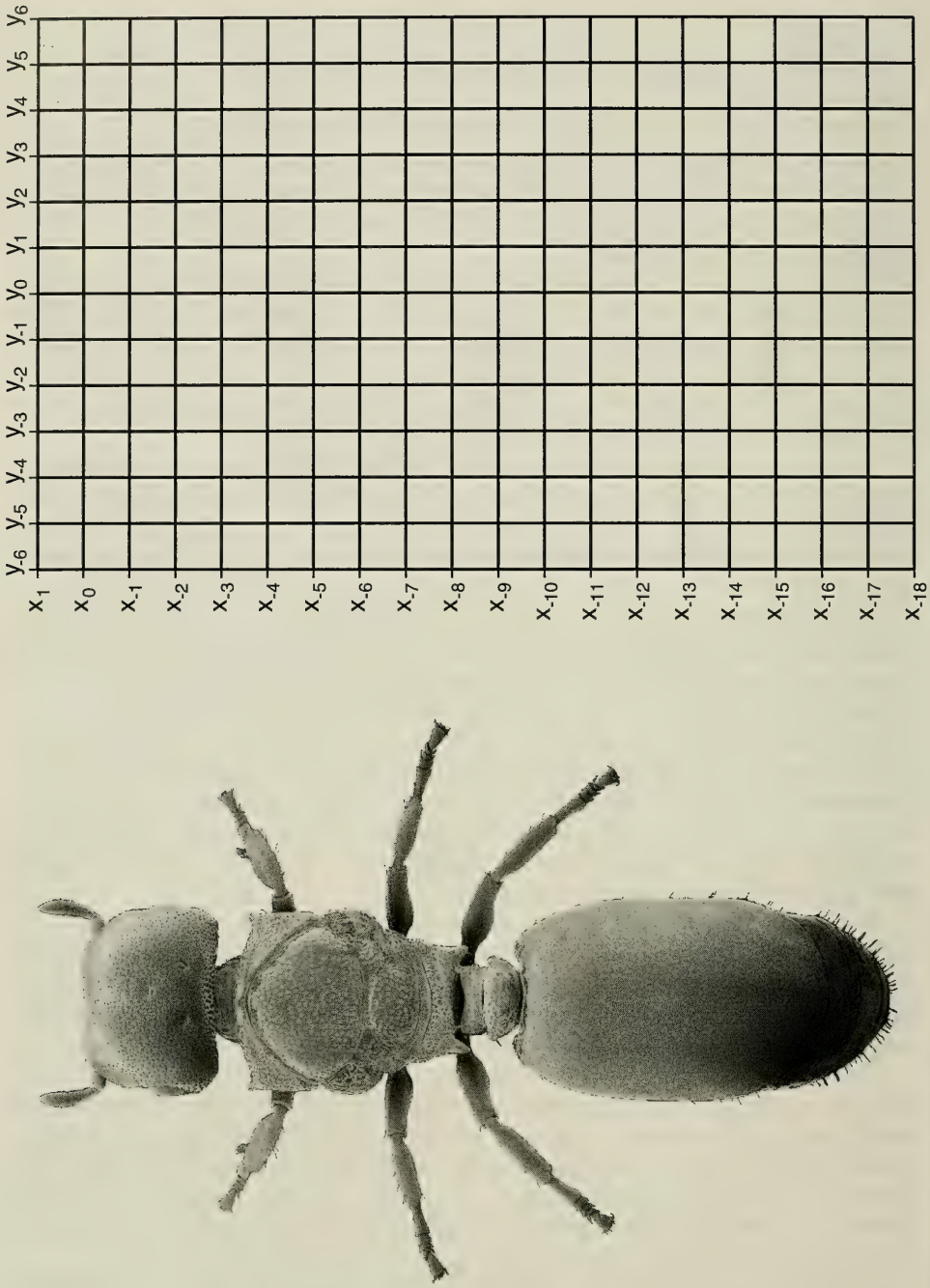
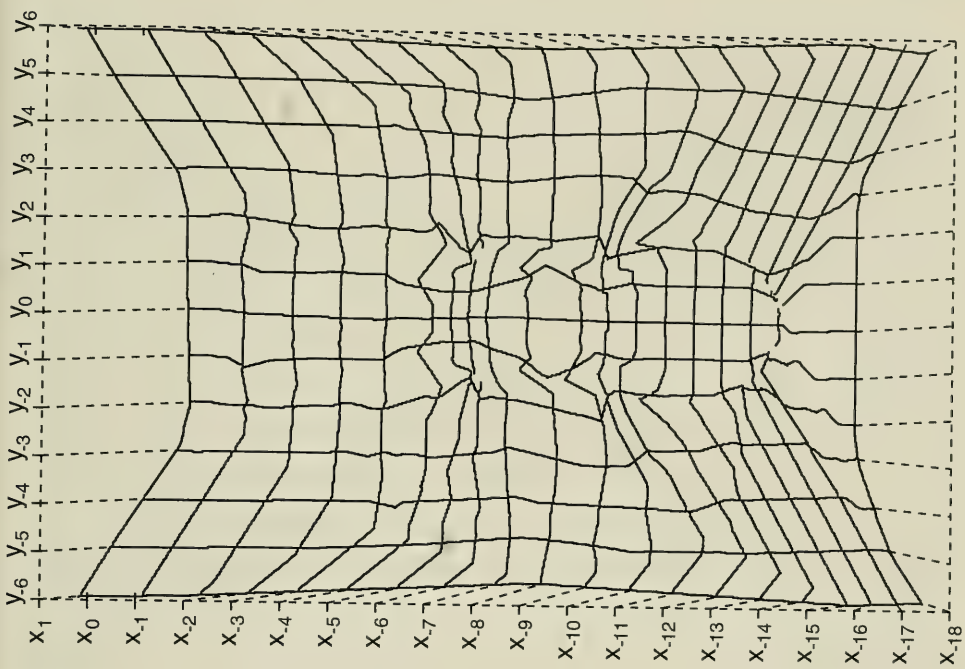


Fig. 364. *Cephalotes pusillus* (KLUG), gyne with the relative untransformed grid.



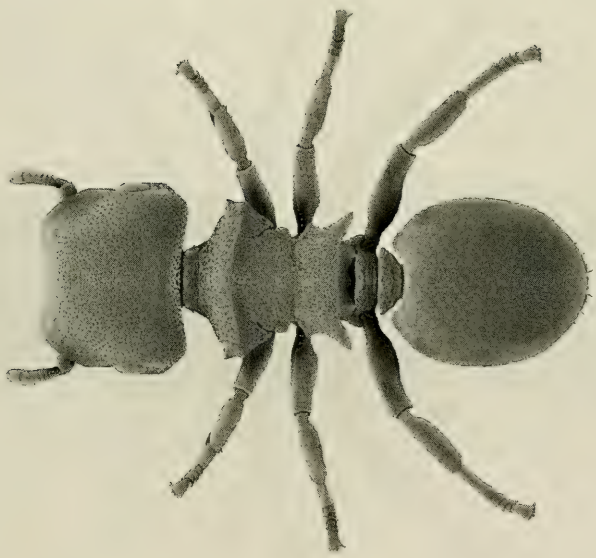


Fig. 365. *Cephalotes pusillus* (KLUG), soldier with the relative transformed gyne grid.

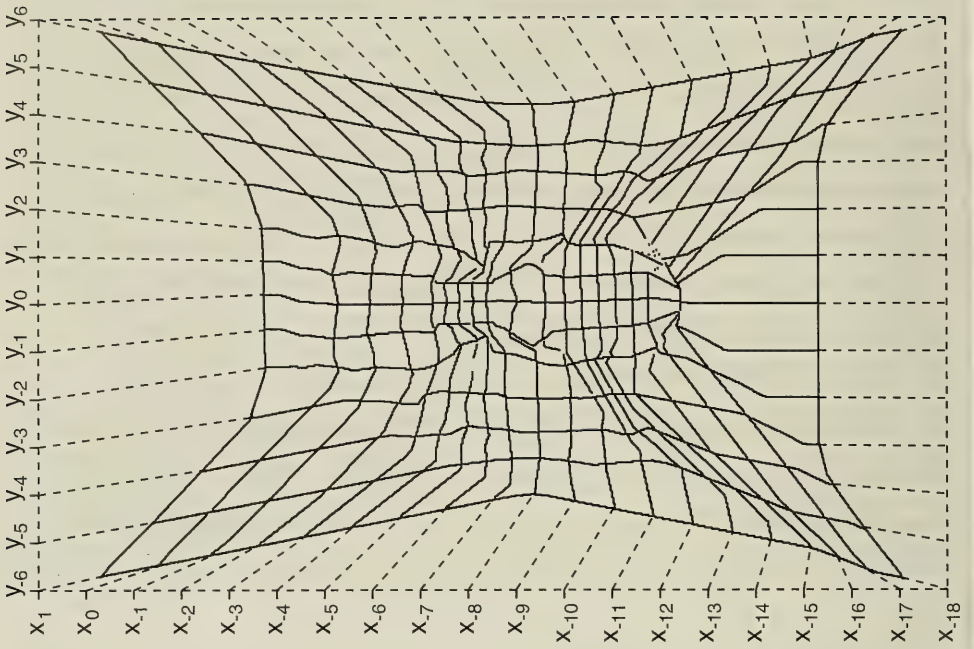


Fig. 366. *Cephalotes pusillus* (KLUG), worker with the relative transformed gyne grid.

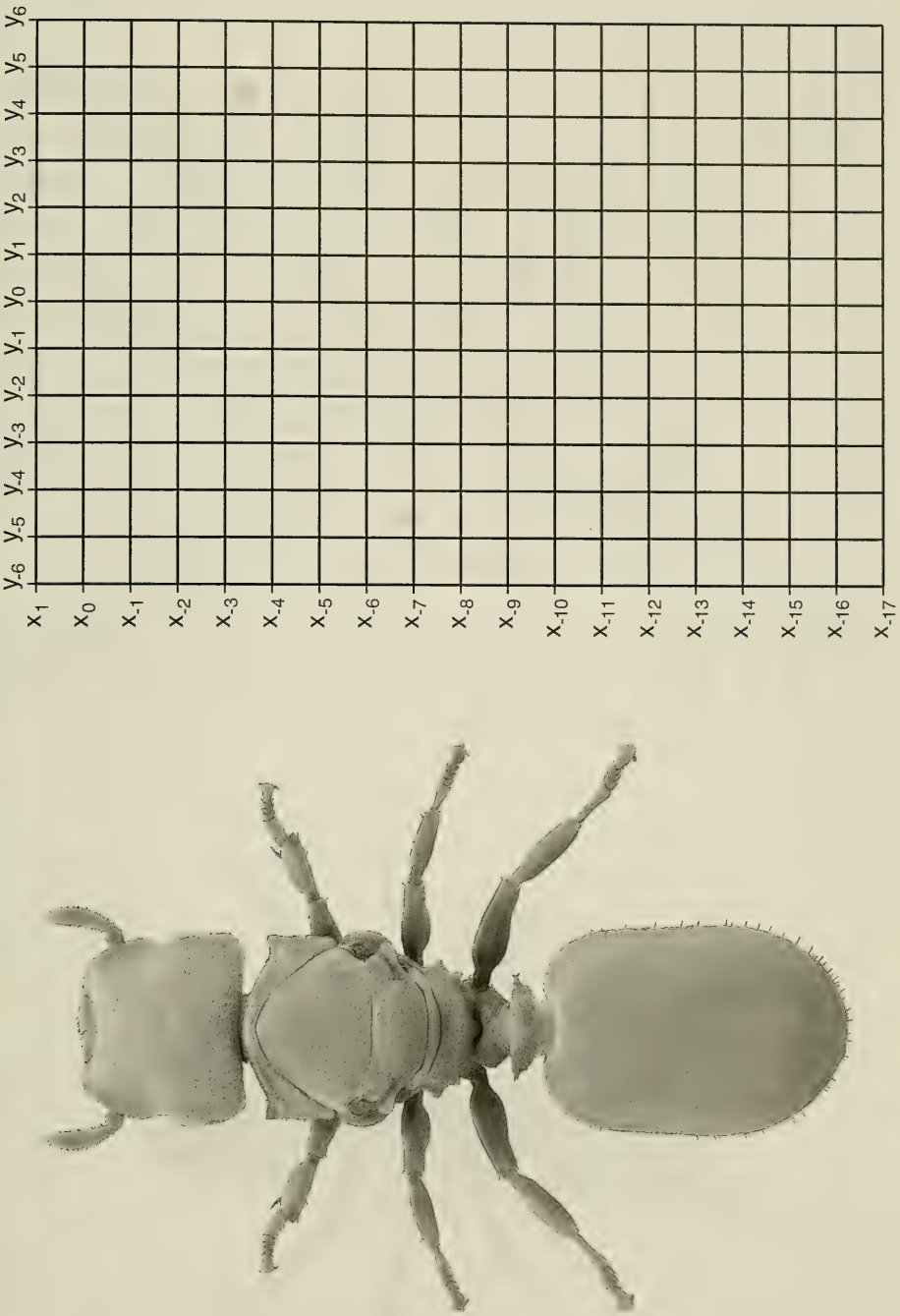


Fig. 367. *Cephalotes borgmeieri* (KEMPF), gyne with the relative untransformed grid.

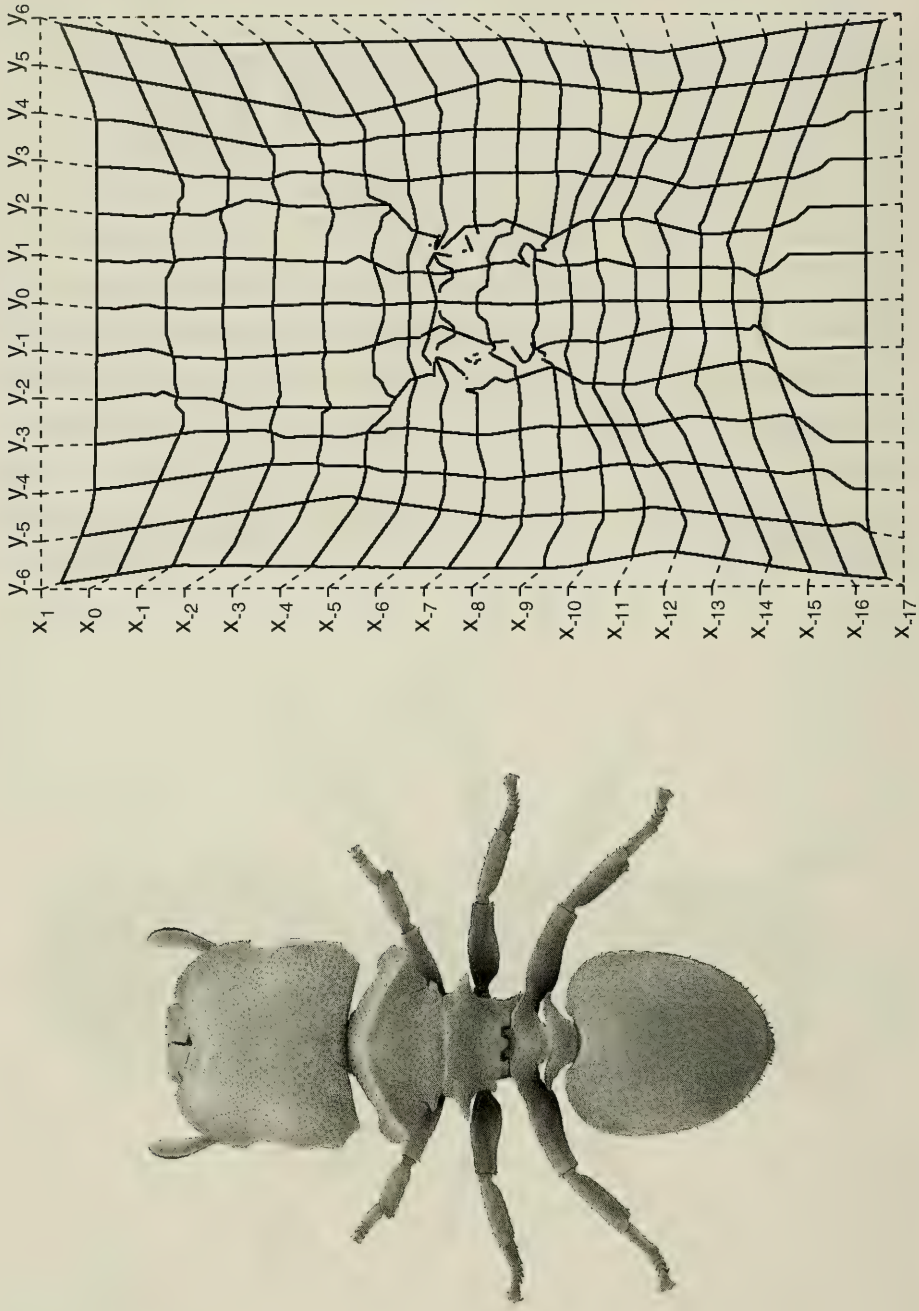


Fig. 368. *Cephalotes borgmeieri* (Kempf), soldier with the relative transformed gyne grid.

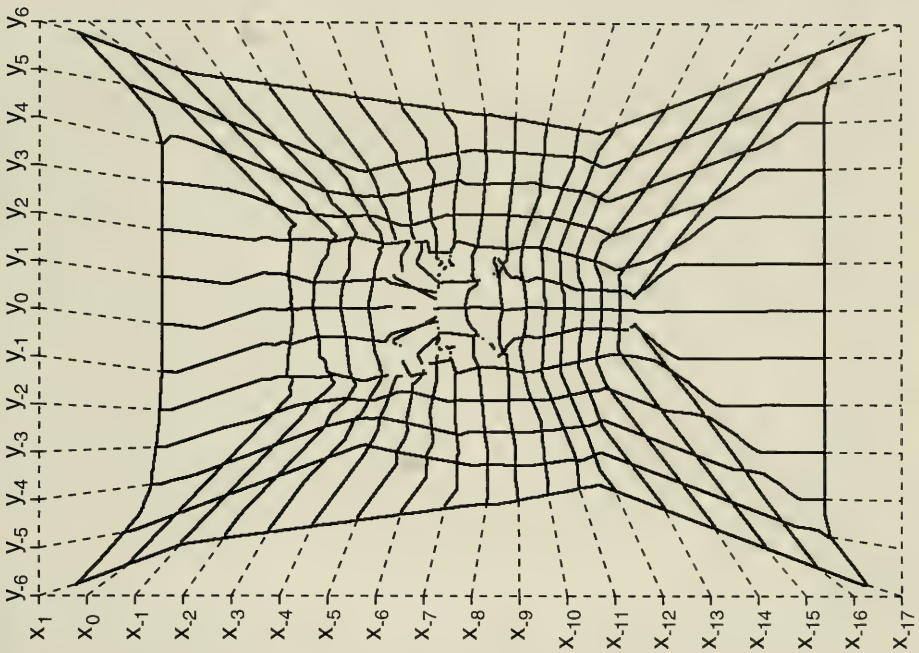


Fig. 369. *Cephalotes borgmeieri* (Kempf), worker with the relative transformed gyne grid.

We think it reasonable to tentatively extend these conclusions to all the other species and clades listed at the beginning of this chapter.

6.4.1.3. Two-caste system with disc-bearing soldiers

Most of the remaining species of *Cephalotes* for which the soldier is known also possess two neuter castes. However, the head of the soldier bears, in addition, a flat, disc-shaped structure covering most of the head as seen in frontal view. Exceptions to this rule are four species of the *pavonii* clade (*betoi*, *borgmeieri*, *depressus* and *eduarduli*), two species of the *multispinosus* clade (*goniodontus* and *multispinosus*), *membranaceus*, and the rather isolated *duckei* and *bruchi* (representing a clade of its own); these species show incomplete cephalic discs. The cephalic disc, in general, is to be found not only in the soldiers, but also in the great majority of the gynes of the same species. Only the remaining three species of the *pavonii* clade (*cordatus*, *pavonii* and *cristatus*) appear to occupy an intermediate position in the evolution of the head disc: their soldiers have a fully developed disc and the gynes bear an incomplete disc. The discovery of a fossil soldier of *C. olmecus* in Mexican amber and indirect cladistic evidence drawn from the position of some of our fossil species in the *Cephalotes* phylogeny show that both, the two-caste system and the cephalic disc of the soldier, had been selected already prior to amber times.

For the biometric description of the castes of these ants we had at our disposal a colony of *C. angustus*.

The frequency distributions of our standard measurements (pronotal width and hind tibia length) show a wide overlap between castes with respect to tibial length. The figures 370 and 371 show that there is little overlap between gynes and workers in hind tibia length and no overlap at all between workers and soldiers in pronotal width; soldiers, in addition, have much wider pronota than gynes. In *angustus* we find the reverse of the biometric relations we found in *pusillus*: in the latter species the soldiers are intermediate in (some) body measurements between gynes and workers, while, in *angustus*, soldiers are the largest individuals and gynes are intermediate between them and workers. Size separation between castes is even clearer than for the species where the soldiers bear no cephalic disc. The relative deviations from the normal of the frequency distributions of the body parts we measured are as follows:

	pronotal width		hind tibia length	
	skewness	kurtosis	skewness	kurtosis
gynes	–0.430	–0.191	–0.533	0.113
soldiers	–0.566	–0.184	0.164	–0.720
workers	–0.253	–0.328	–0.348	0.367

Plotting the same measures in pairs (Fig. 372) and testing the degree of fit of a set of models of increasing complexity gives the following adjusted R^2 values:

Regression	Gyne	Soldier	Worker
Simple, rough data	0.214	0.350	0.780
Simple, log transformed data	0.211	0.356	0.790
Polynomial, degree 2	0.191	0.384	0.777
Polynomial, degree 3	0.176	0.391	0.776

Once more simple regression accounts sufficiently well for intra-caste variation, though all the R^2 values are very low.

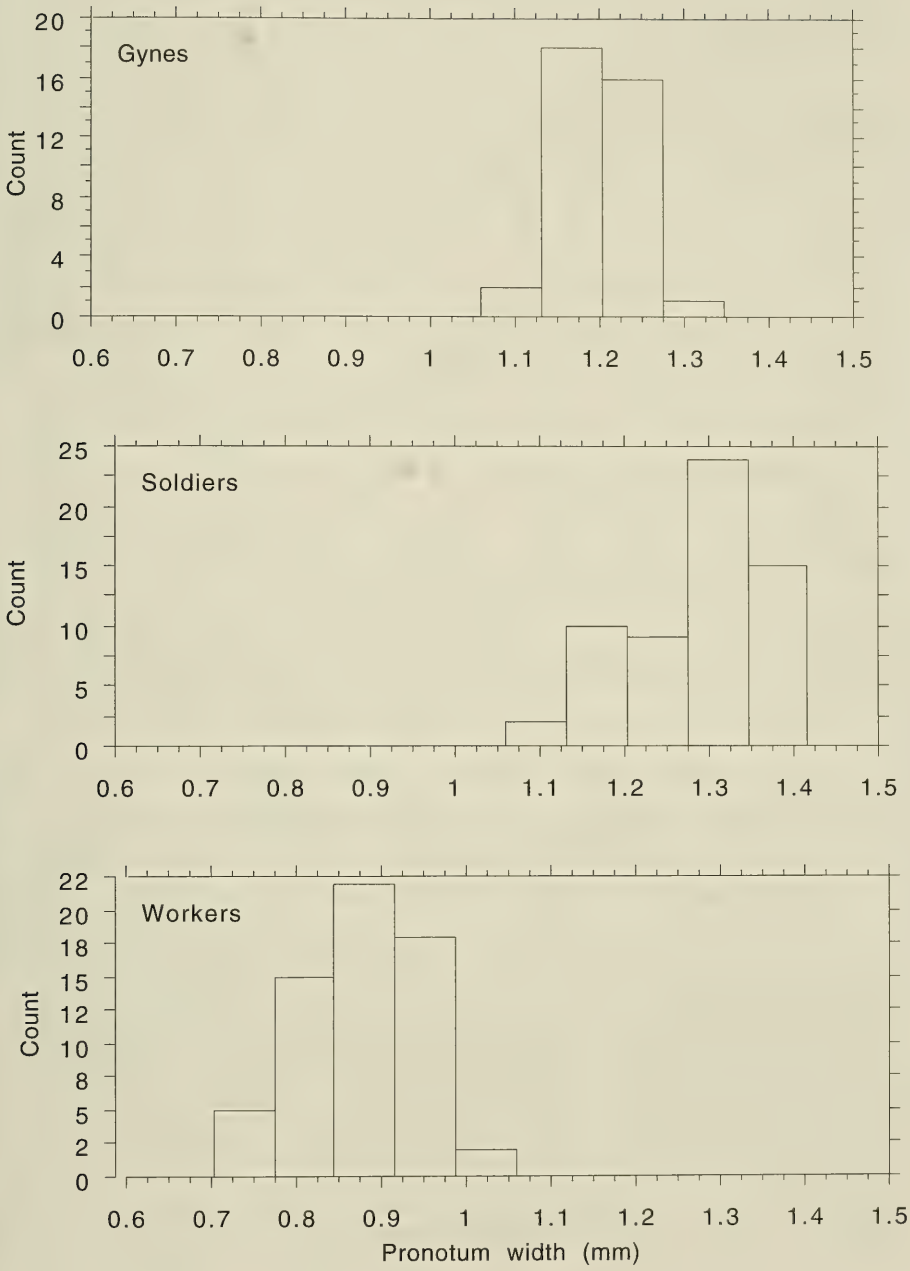


Fig. 370. *Cephalotes angustus* (MAYR). Frequency distributions of the maximum pronotal width of a sample of the three female castes from a single colony from Botucatu (São Paulo).

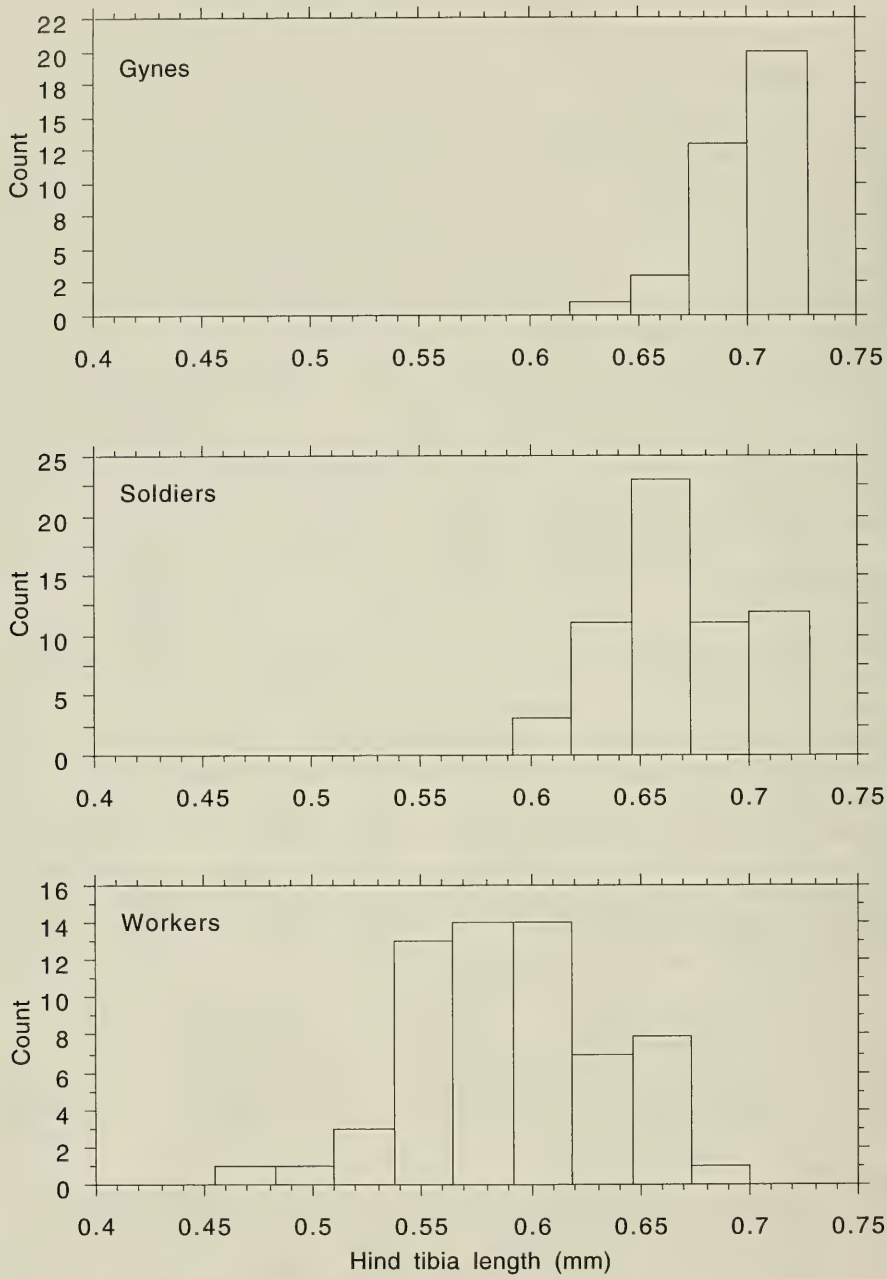


Fig. 371. *Cephalotes angustus* (MAYR). Frequency distributions of the hind tibia length of a sample of the three female castes from a single colony from Botucatu (São Paulo).

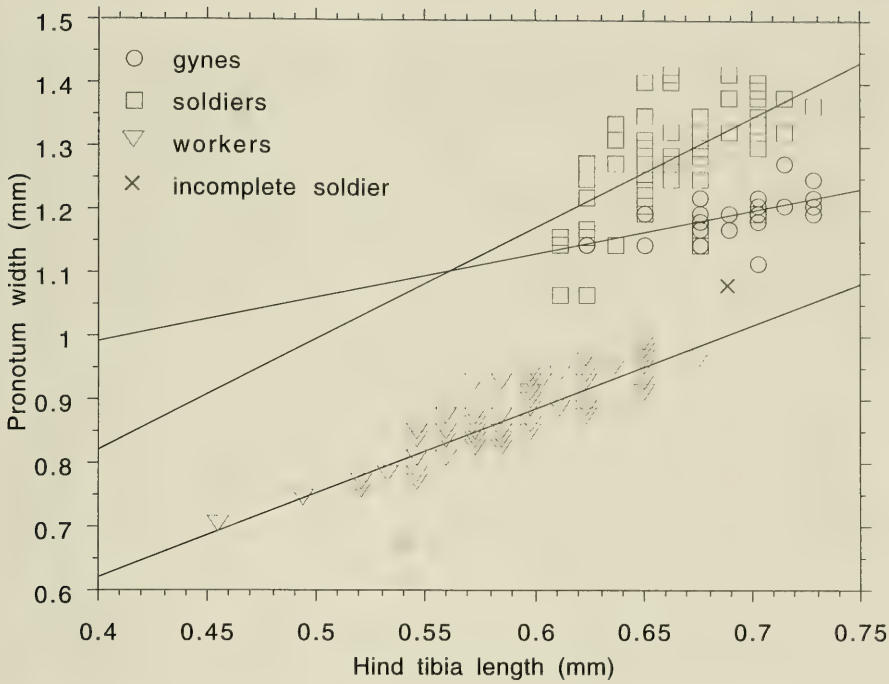


Fig. 372. *Cephalotes angustus* (MAYR). Scattergram and relative regression lines of the maximum pronotal width and hind tibia length of a sample of females from a single nest from Botucatu (S. Paulo) divided by caste.

The regression equation (figures in brackets are 2 x Standard Error) is for gynes:
Pronotum width = 0.716 [±0.292] + 0.691[±0.420] x (Hind tibia length)
for soldiers:
Pronotum width = 0.116 [±0.408] + 1.759 [±0.614] x (Hind tibia length)
and, for workers:
Pronotum width = 0.094 [±0.106] + 1.322 [±0.180] x (Hind tibia length).

In a manner similar to what we already observed for *pusillus*, but contrary to expectation based on morphology, the regression lines (Fig. 372) show substantially similar patterns for both workers and soldiers. Both neuter castes are biometrically different from gynes which, on account of size alone, appear intermediate between workers and soldiers. This, despite the fact that, morphologically, gynes are much closer to soldiers than the latter are to workers. Disc-bearing soldiers of *angustus* are a kind of "supergynes" with respect to body size and general morphology. Statistically, the regression line of gynes does not differ from that of soldiers but it differs from that of workers in both intercept and slope confirming the morphological difference observed visually.

C. angustus castes also appear to be much better characterised by morphology than by biometry. A superficial biometric description suggests gynes as being intermediate between workers and soldiers (as they really are if one considers size alone) but simple regression analysis is sufficient for an initial separation of gynes from both neuter castes.

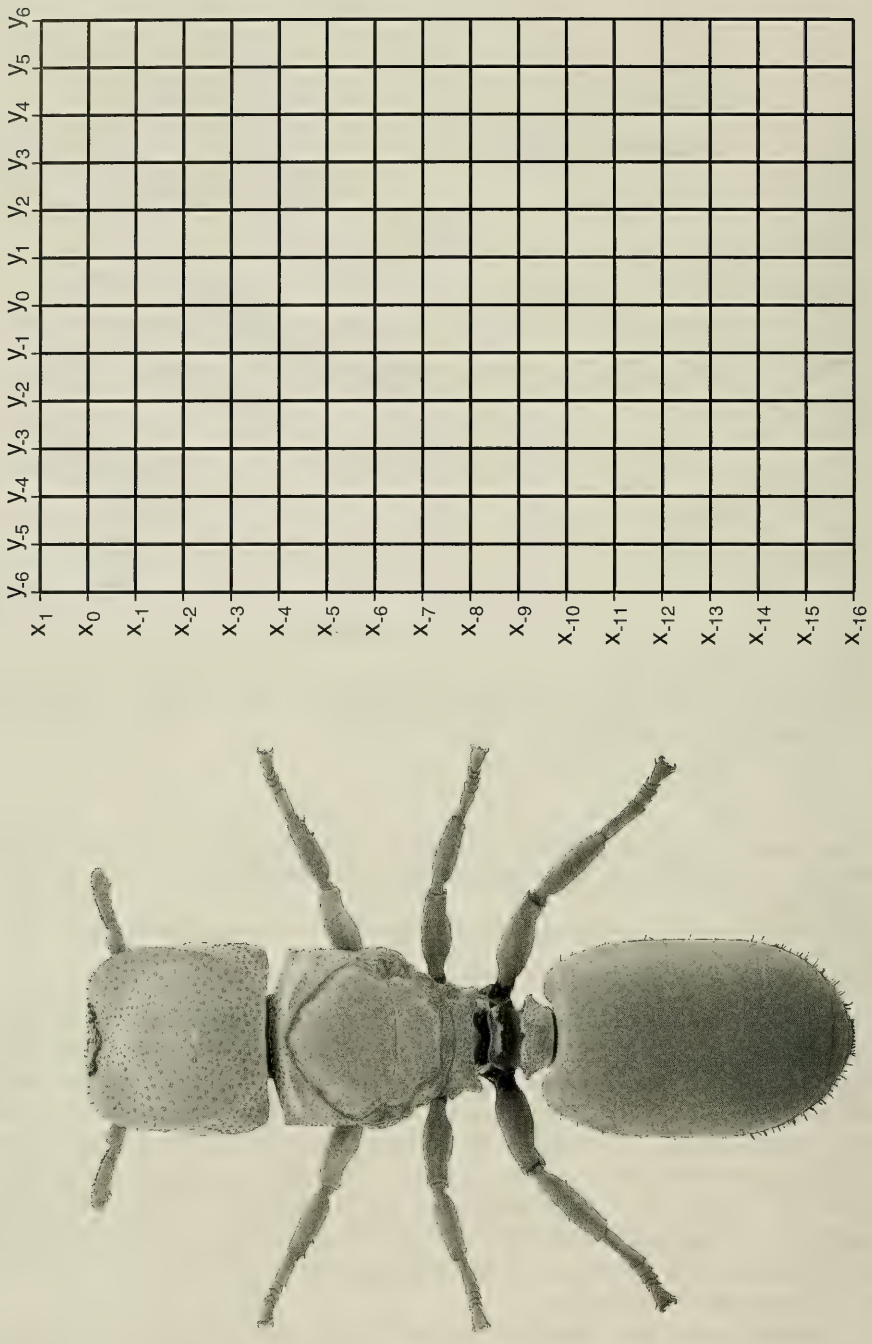
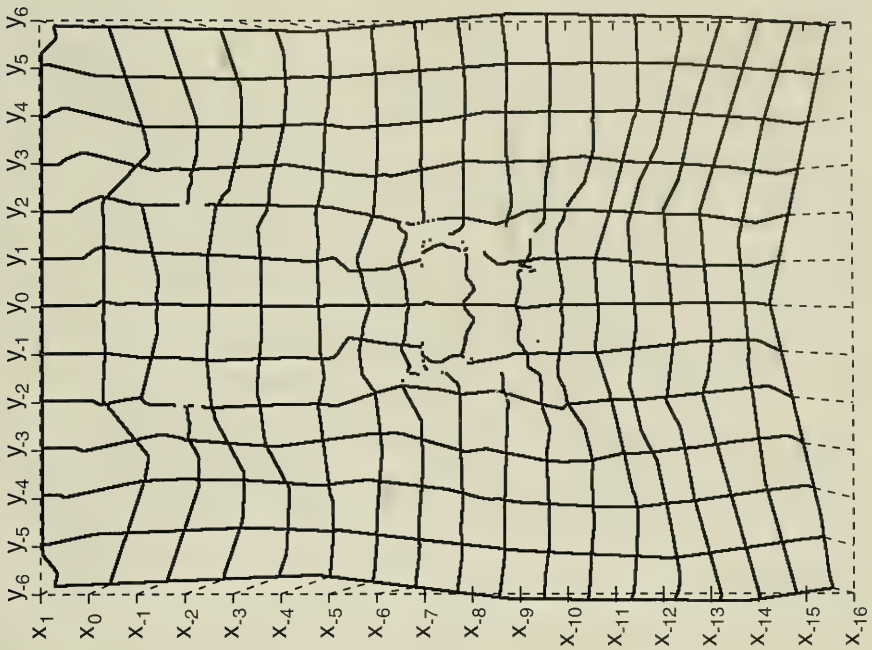


Fig. 373. *Cephalotes angustus* (MAYR), gyne with the relative untransformed grid.



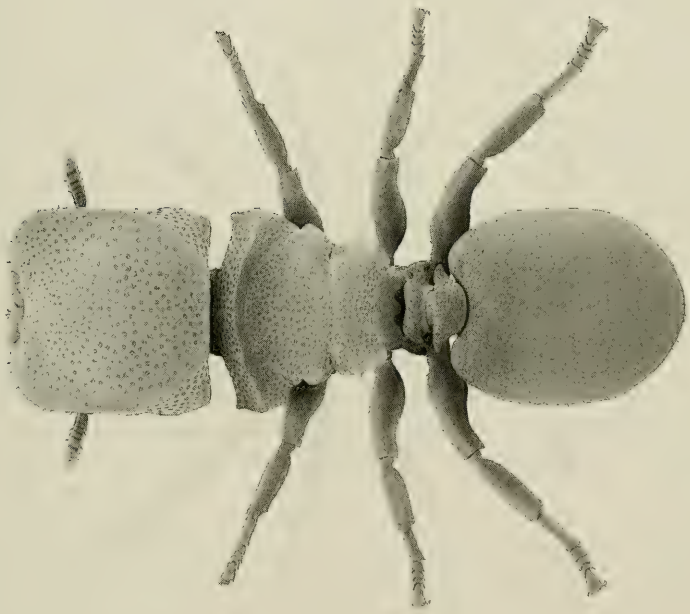


Fig. 374. *Cephalotes angustus* (MAYR), soldier with the relative transformed gyne grid.

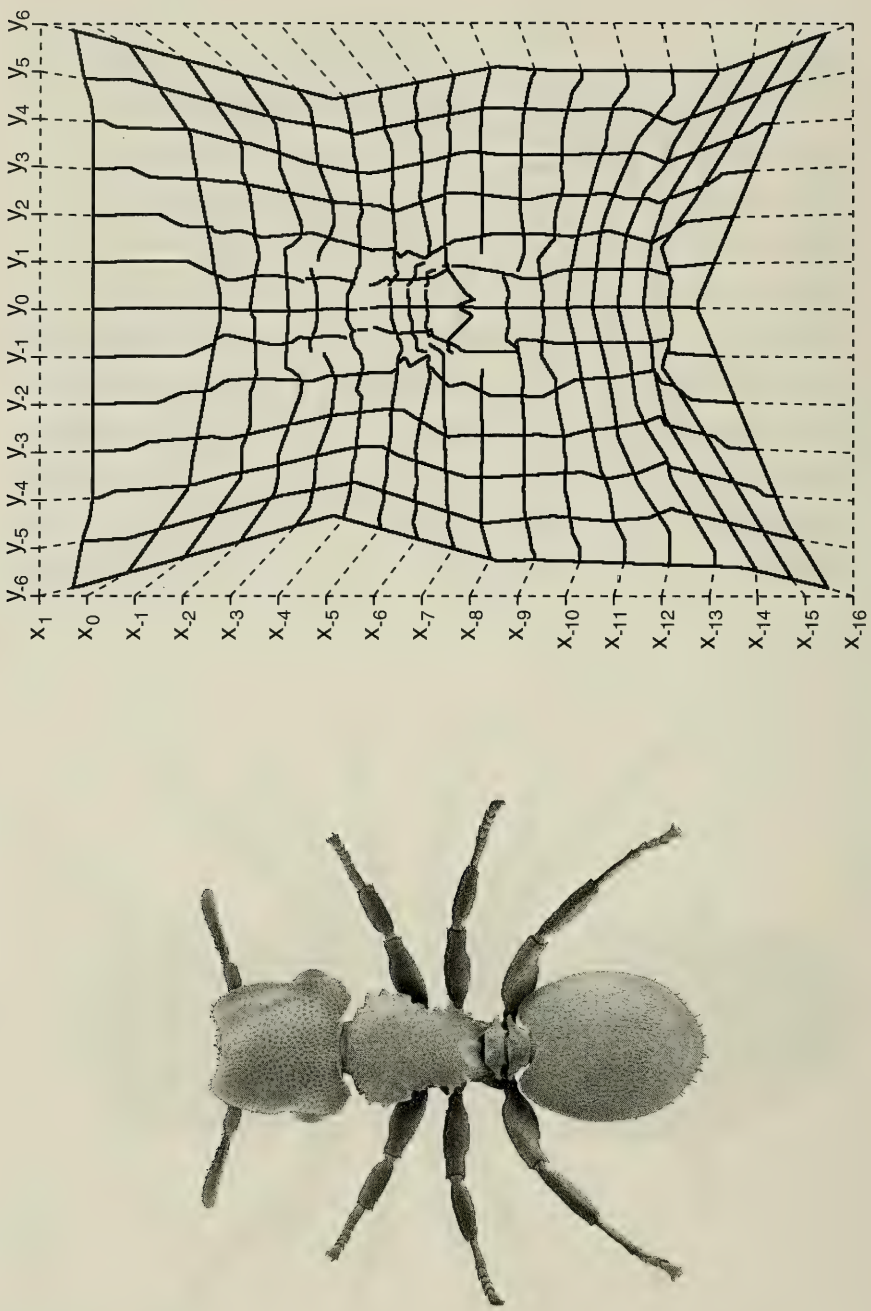


Fig. 375. *Cephalotes angustus* (MAYR), worker with the relative transformed gyne grid.

We first considered *angustus* as possessing a caste system different from that of the other *Cephalotes* based on the presence of the disc-shaped head. Now a second, important character distinguishes the caste system of this species: the presence of soldiers with head and mesosoma larger than those of gynes. Visual examination of all known species of the genus suggests that this character is universal for those species with a disc-shaped head.

The transformation grids for the three castes of *C. angustus* are given in Figs. 373, 374 and 375. The transformed grid for the soldier of this species confirms our previous biometric results: not only the homologous cephalic fields already mentioned for *borgmeieri* appear enlarged in a similar manner, but the true abdomen (i. e. propodeum, peduncle and gaster) and at least the hind legs are subject to a slight broadening and a slight elongation in the case of the legs. This results in a divergence of most (parts of the) y ordinates which often overlap and cross distally the primitive gyne condition. Most remaining differences with the grid of the *borgmeieri* soldier appear to be simply size-dependant.

The *angustus* worker grid is also very similar to the one of *borgmeieri*. The differences visible in the fields $y_3 - y_{-3}$, and $x_{-5} - x_{-7}$ can be largely explained by a reduction of the pronotal lamellae in the first species and a development in the second.

6.4.2. Behavioural specialisation and function of the soldiers

There is abundant evidence, both assumed and anecdotal, that the function of the soldiers is essentially that of defence. More detailed laboratory studies on the behaviour of these ants failed either to confirm or to deny this function. According to WILSON (1976 b) the soldiers of *C. varians* do not exercise any particular function and rely exclusively on food regurgitated by the workers.

WILSON (1976 b) published the ethogram (i. e. a "complete catalogue of the behavioural patterns") for *C. varians*. From this analysis it appears that soldiers spend over 40% of their active time in regurgitating food with other individuals, and 34% in self-grooming. These results are confirmed by those of COLE (1980, 1983 b) who, for the same species, states that the soldiers invest 56% of their time in self-grooming and the remaining 44% in regurgitating food with workers. Unfortunately these studies make no mention of the entrance-plugging function of the soldiers (i. e. the main function to which this caste is supposed to be destined) presumably either because they did not consider it as a behavioural act or because all the colonies on which these observations have been made were kept in glass tubes in which the ants did not exercise this behaviour.

Another fact worthy of mention here is that even if the entrance plugging function of the soldiers is assumed as demonstrated both under natural conditions and in laboratory colonies, this caste appears to be numerically over-represented for performing this sole function.

To explore the possibility and the importance of an entrance watching function of the soldiers, we observed in the laboratory during several days the large fragment of the Brazilian colony of *C. pusillus* (a species with distinct two castes system but without disc-bearing soldiers) already mentioned in the material chapter and what we regard as a complete or nearly complete colony of *C. angustus* (a species with disc-bearing soldiers).

We report the results of our observations on these species sequentially.

At the time of our observations the *pusillus* colony consisted of 1,617 workers, 512 soldiers and several larvae and pupae. Preliminary qualitative observations on the nest showed the regular presence of soldiers in and around the nest entrance, but did not suggest a particular overrepresentation of this caste. On the contrary, workers were often more numerous than soldiers among the individuals staying around the nest entrance. The caste composition of the laboratory colony was 76% workers and 24% soldiers making it likely that fewer representatives of the latter category should have been encountered among the entrance guarding individuals.

Tab. 4. Absolute numbers and relative frequencies (in percent) of soldiers and workers of *Cephalotes pusillus* at the "nest entrance watching" function recorded during 23 observations under the laboratory conditions described in the text. Distance between two consecutive observations 2 hours or more. The alternate unshaded and shaded bands indicate the various consecutive days on which the observations have been made. The observations continued until only marked soldiers had been encountered.

Observation	No. workers	% of all workers	No. soldiers	% of all soldiers
1	35	*2.16*	3	*0.59*
2	29	*1.79*	9	*1.76*
3	22	*1.36*	8	*1.56*
4	22	*1.36*	8	*1.56*
5	21	*1.30*	14	*2.73*
6	35	*2.16*	22	*4.30*
7	37	*2.29*	15	*2.93*
8	30	*1.86*	20	*3.91*
9	21	*1.30*	23	*4.49*
10	31	*1.92*	20	*3.91*
11	34	*2.10*	28	*5.47*
12	27	*1.67*	36	*7.03*
13	27	*1.67*	25	*4.88*
14	19	*1.18*	15	*2.93*
15	13	*0.80*	19	*3.71*
16	29	*1.79*	41	*8.01*
17	52	*3.22*	50	*9.77*
18	37	*2.29*	32	*6.25*
19	31	*1.92*	26	*5.08*
20	48	*2.97*	47	*9.18*
21	32	*1.98*	35	*6.84*
22	19	*1.18*	32	*6.25*
23	20	*1.24*	25	*4.88*

During our counts we recorded the presence of 19–52 workers and 3–50 soldiers staying in or close to the nest entrance.

Our observations consisted of counting at various times the numbers of workers and soldiers staying at least several minutes (i. e. not simply passing through) in or within 1 cm distance from the nest entrance. The observations continued over the course of 5 days at irregular intervals of more than two hours in order to allow for

the natural turnover of the colony population after each observation. The results of 23 such counts are reported in Table 4.

The variance component estimates (variance estimate between days 0.385, residual variance 0.141, F ratio = 13.44, p> 0.0) indicate a greater variation between than within days, i. e. there is no appreciable circadian rhythm in the entrance watching function. Our results suggest, moreover, that a worker has about half the probability of a soldier to take part to the "entrance watching function" (mean odds-ratio = -0.821, $\sigma = \sqrt{0.141}$, $e^{-0.821+\frac{1}{2}\sqrt{0.141}} \approx 53\%$).

Tab. 5. Absolute numbers and relative frequencies (in percent) of soldiers and workers of *Cephalotes angustus* engaged in the "nest entrance watching" function recorded during 11 observations under the laboratory conditions described in the text. Time between two consecutive observations was 2 hours or more. The alternate unshaded and shaded bands show the various consecutive days on which the observations were made. The observations continued until only marked soldiers had been encountered.

Observation	No. workers	% of all workers	No. soldiers	% of all soldiers
1	3	*0.79*	3	*2.11*
2	5	*1.32*	6	*4.23*
3	1	*0.26*	8	*5.63*
4	4	*1.06*	6	*4.23*
5	1	*0.26*	6	*4.23*
6	4	*1.06*	6	*4.23*
7	4	*1.06*	5	*3.52*
8	4	*1.06*	5	*3.52*
9	6	*1.59*	6	*4.23*
10	0	*0*	5	*3.52*
11	0	*0*	4	*2.82*

To see whether a different soldier morphology implies a different division of tasks among castes taking part in the entrance watching function, we repeated the observations on an *angustus* colony consisting of 378 workers, 142 soldiers, several larvae and pupae, a few males and winged gynes and two dealate gynes. The worker/soldier ratio was almost 4:1, i. e. *a priori* one should expect to find 4 more workers than soldiers involved in any task. *C. angustus*, of course, is a species whose soldiers bear a fully developed disc.

The results of 11 counts of the ants staying in or immediately outside the nest entrance and conducted as for *C. pusillus* are reported in Table 5.

During our observations we recorded the presence of 0–6 workers and 3–8 soldiers staying in or close to the nest entrance. These figures are much smaller than those we recorded for *C. pusillus*, both absolutely and proportionally. They are, however, perfectly comparable to those we recorded in a similar experimental situation on a small fragment of a colony of *C. targionii*, another species with disc-bearing soldiers. We do not report the results of our observations on *targionii* here because of the fragmentary condition of the colony on which the observations were conducted.

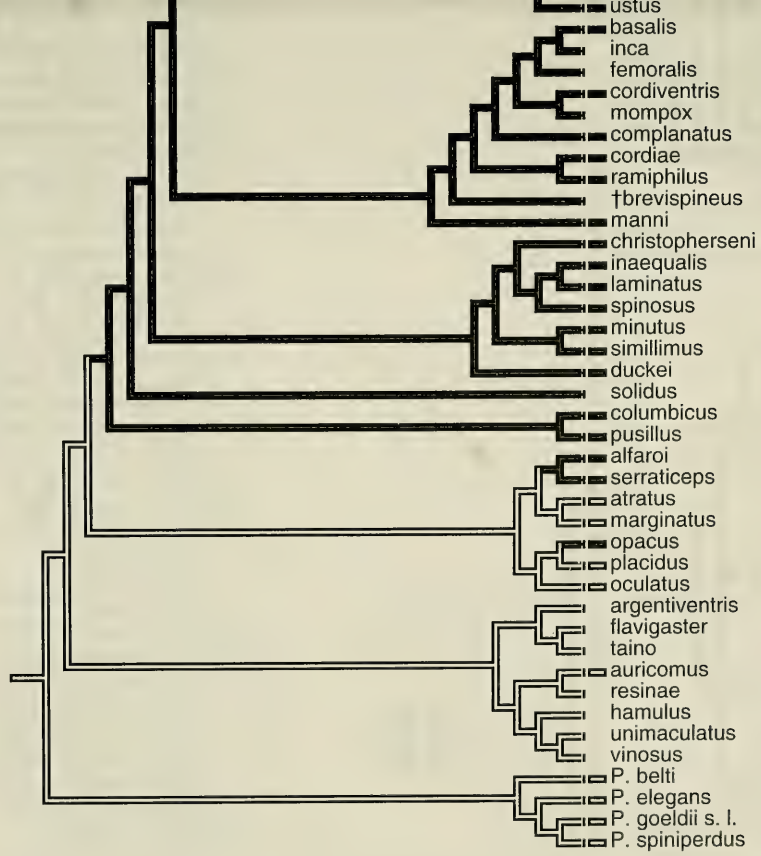
The variance component estimates (variance between days 0.165, residual variance 1.321, F ratio = 1.455, p = 0.289) shows greater circadian variation than between days variation,though the difference is not statistically significant.The mean odds-ratio is –2.12 and $\sigma = \sqrt{1.32}$ with $e^{-2.12 + \frac{1}{2}\sqrt{1.32}} \approx 21\%$. I. e., in *angustus*, a worker has only 21% chance of a soldier in participating the nest entrance watching function.

These results are very symbolic since they suggest that species in which the soldier have no morphological adaptation for phragmosis allow (need?) more workers to take part in this function than those species in which the soldiers bear the cephalic disc. We regard this conclusion as being suggestive at this stage, given the size of our sample: we studied this behaviour in only two out of more than 100 known species. It would be particularly interesting to repeat our observations on a species of the *hamulus* clade where, according to our cladogram, soldiers are plesiomorphically absent but where the entrance blocking function is exercised by the workers as we observed in the field for *C. auricomus*. In particular, ascertaining if workers watching the nest entrance perform this task by chance alone or if they belong to a behaviourally specialised subcaste would allow new insights in the origin of soldiers in *Cephalotes*.

As we wrote in the methods chapter, the proportion of soldiers (and of workers) actually devoted to nest entrance watching, under natural conditions, is likely to be much greater than those recorded in our laboratory observations. The number of individuals devoted to this task should be a function of both the number of nest entrances and of their size. The natural nest from which our *angustus* laboratory colony originated was located in abandoned tunnels dug by beetle larvae in a *Caesalpinia* tree. We counted at least 10 different entrances of a size slightly smaller than that of the experimental nest (10 mm diameter). During our observation period over a nest with a single entrance, we marked the soldiers staying in the nest entrance. All together, they represented 26 out of the 142 soldiers present in the colony, i. e. 18% of the total soldier population. It can be easily deduced that in a natural situation of a nest with 10 entrances, the whole soldier population may be alternatively engaged in this task.

The results of our observations show that the entrance guarding function can be regarded as one of the primary tasks of the soldier caste even in the absence of its most spectacular morphological correlate, the head disc. Nonetheless, the number of soldiers devoted to this task at each instant during our observations varied between 0.6 and 9.8% of the total soldier population. Our findings show a relatively low turnover rate of the individuals performing this function: 3–5 days appear to be necessary to involve all individuals devoted to the entrance watching function. This is only true, however, if, during our observations, we really marked all the entrance watching soldiers.

For this reason we tested the possibility that only a numerically small subset of soldiers may be devoted to this task as our results seemed to suggest. The hypothesis was tested by marking all the soldiers we observed at the nest entrance during our counts. Our observations (conducted at the same time and on the same nests as those reported in Tables 4 and 5) continued until only marked soldiers were observed at the nest entrance.


ustus
basalis
inca
femoralis
cordiventris
mompox
complanatus
cordiae
ramiphilus
†brevispineus
manni
christopherseni
inaequalis
laminatus
spinosus
minutus
simillimus
duckei
solidus
columbicus
pusillus
alfaroi
serraticeps
atratus
marginatus
opacus
placidus
oculatus
argentiventris
flavigaster
taino
auricomus
resinae
hamulus
unimaculatus
vinosus
P. belti
P. elegans
P. goeldii s. l.
P. spiniperdus

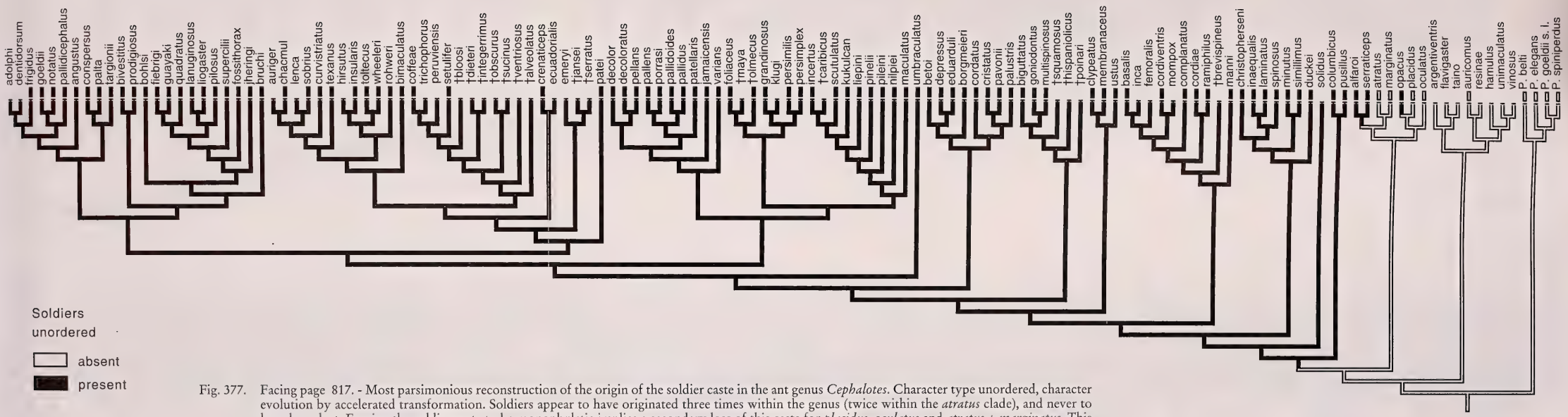
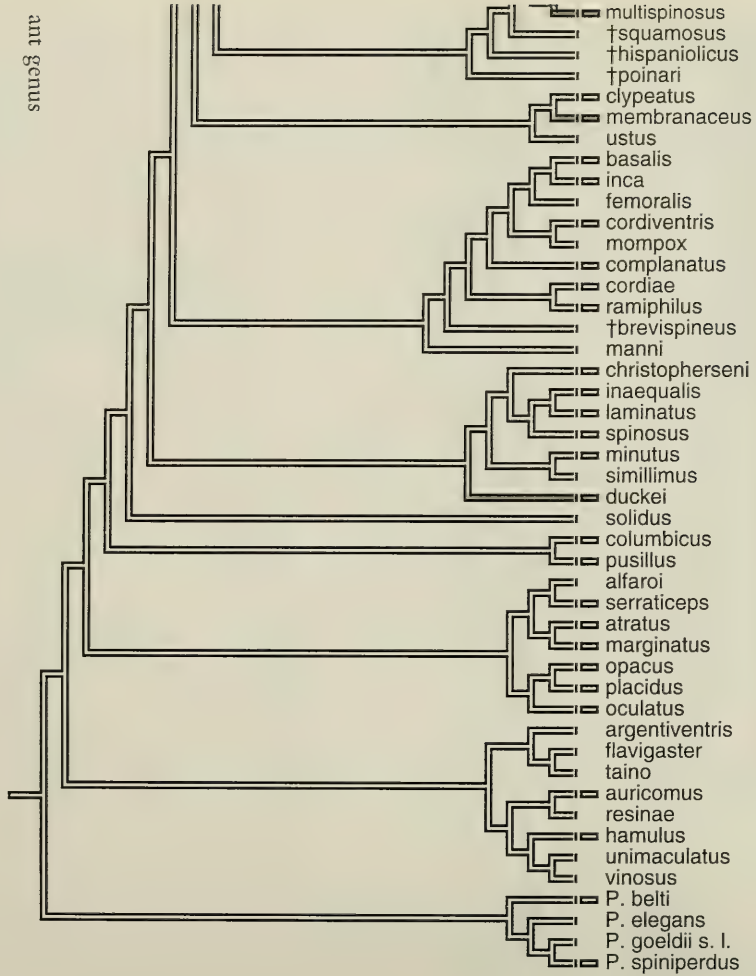


Fig. 377. Facing page 817. - Most parsimonious reconstruction of the origin of the soldier caste in the ant genus *Cephalotes*. Character type unordered, character evolution by accelerated transformation. Soldiers appear to have originated three times within the genus (twice within the *atratus* clade), and never to have been lost. Forcing the soldier caste to be monophyletic implies a secondary loss of this caste for *placidus*, *oculatus* and *atratus* + *marginatus*. This alternative hypothesis needs only one additional evolutionary step.


multispinosus
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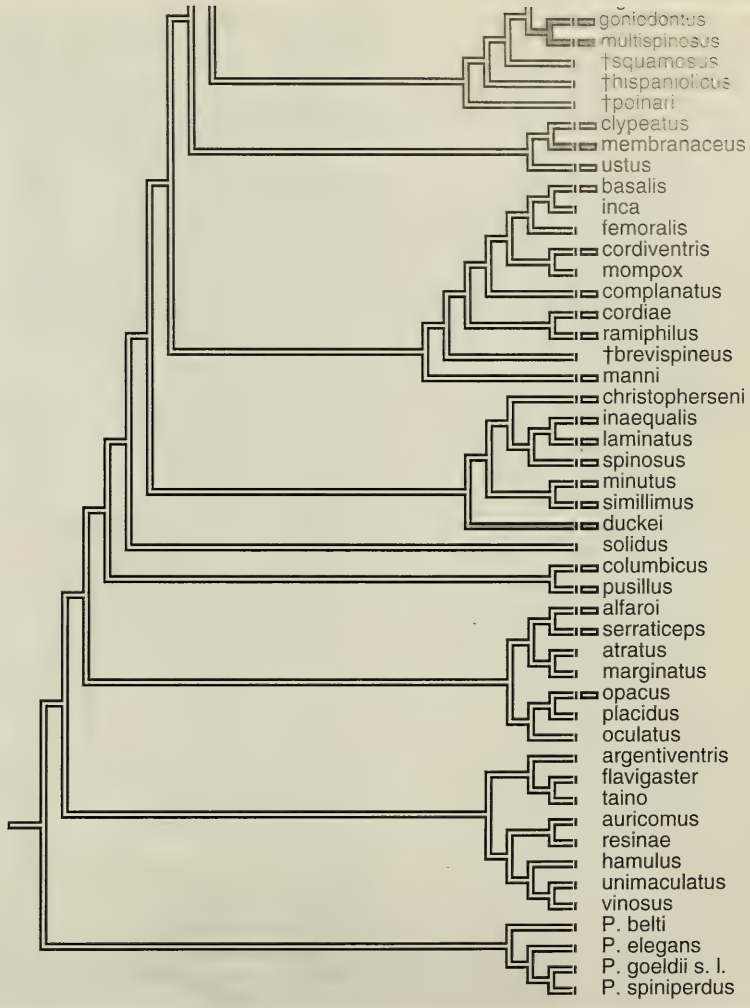
†hispaniolicus
†poinari
clypeatus
membranaceus
ustus
basalis
inca
femoralis
cordiventris
mompox
complanatus
cordiae
ramiphilus
†brevispineus
manni
christopherseni
inaequalis
laminatus
spinosus
minutus
simillimus
duckei
solidus
columbicus
pusillus
alfaroi
serraticeps
atratus
marginatus
opacus
placidus
oculatus
argentiventris
flavigaster
taino
auricomus
resinae
hamulus
unimaculatus
vinosus
P. belti
P. elegans
P. goeldii s. l.
P. spiniperdus


goniodontus
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†squamosus
†hispaniolicus
†poinari
clypeatus
membranaceus
ustus
basalis
inca
femoralis
cordiventris
mompox
complanatus
cordiae
ramiphilus
†brevispineus
manni
christopherseni
inaequalis
laminatus
spinosus
minutus
simillimus
duckei
solidus
columbicus
pusillus
alfaroi
serraticeps
atratus
marginatus
opacus
placidus
oculatus
argentiventris
flavigaster
taino
auricomus
resinae
hamulus
unimaculatus
vinosus
P. belti
P. elegans
P. goeldii s. l.
P. spiniperdus

ant genus

We reached this result in the *pusillus* colony after 23 observations and, during the whole observation time, we marked 182 soldiers; in the *angustus* colony, we encountered just marked soldiers after 11 observations and we marked a total of 26 soldiers. The fact that following 23 (*pusillus*) and 11 (*angustus*) observations we marked ca. 35% (*pusillus*) and ca. 18% (*angustus*) of the soldier population and that we then encountered only marked soldiers at the nest entrance, supports our starting hypothesis. Using the hypergeometric formula already given in the methods chapter, we computed that the probability of encountering 25 of the 182 marked individuals out of a total of 512 soldiers for *pusillus* and 4 of the 26 marked soldiers out of a colony population of 142 soldiers for *angustus* by chance alone is practically 0.0 in both instances.

In conclusion, "entrance guarding" in *Cephalotes* is a task performed by both workers and soldiers, but more so by soldiers than by workers irrespective of any morphological adaptation for plugging the nest entrance. In the laboratory colonies of both species we studied, only a subset of soldiers was permanently devoted to this task. No other particular soldier task has been detected but it can be readily assumed that under natural conditions, more than one subset of soldiers simultaneously guards more than one nest entrance.

6.4.3. General remarks on the ants' caste system with particular reference to *Cephalotes*

The biometric variation of the workers of the four species we examined appears to be subject to two different rules. The slope of the regression line between pronotal width and hind tibia length is much smaller in *auricomus* (0.76 ± 0.20) than in the other three species examined where the specific slopes overlap each other by between 1.15–1.51. If confirmed by the study of additional species, this difference might contribute to the separation of the *hamulus* clade from the rest of the species dealt within this paper.

We tried to find additional criteria for detecting the presence of different types of female polymorphism within *Cephalotes*. We measured the coordinates of all the intersection points of the transformed grids as described in the methods chapter. The resulting nine sets of 378 coordinates were subjected to Kaiser's image analysis without merging workers and soldiers of the same species into a single variable. The result of the analysis revealed that Factor 1 alone explains 88.6% of the observed variance, Factor 2 explains 9.7% of the observed variance while Factor 3 accounts for only 1.1% of the variance and can be ignored. Surprisingly, the explanatory power of Factor 1 is very similar for all the variables examined and it is Factor 2 what allows a clear division of the variables in two groups: those positively correlated with the factor (*auricomus*, *atratus* minor and *atratus* major) and those negatively correlated with it (all the remaining ones) (Fig. 376).

Caste morphogenesis therefore appears to be much more homogeneous within different castes of the same species than within the same caste of co-generic species. We regard this result as very promising but we are aware that it may be subject to taxonomic bias. *Auricomus* and *atratus*, in fact, are the two basalmost species in the phylogeny of those included in the analysis. The presence of taxonomic bias in our results is a simple hypothesis not supported by the information available to us. In

Fig. 378. Facing page 817. - Most parsimonious reconstruction of the origin of the cephalic disc among soldiers (top) and gynes (bottom) of the ant genus *Cephalotes*. Character type unordered, character evolution by accelerated transformation.

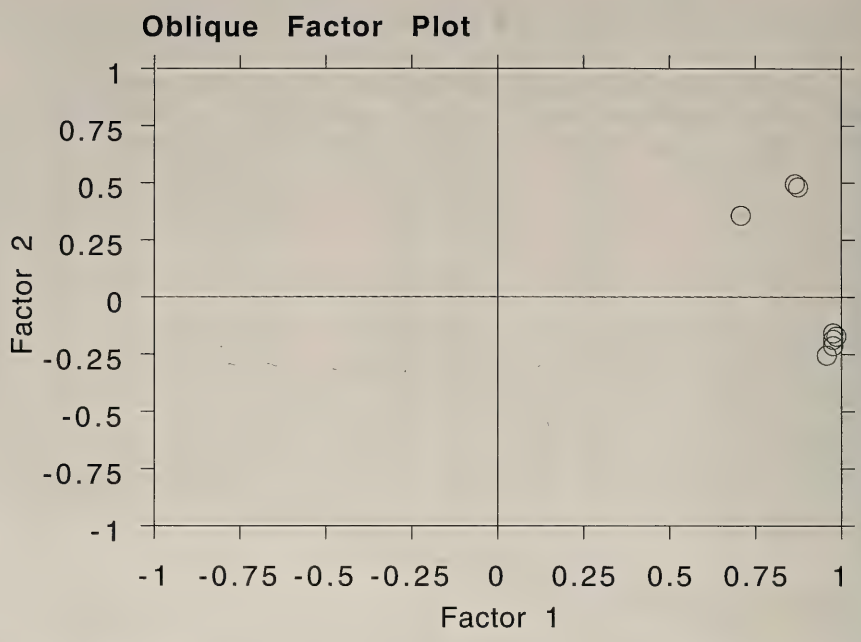

Fig. 376. Plot for the two principal oblique factors resulting from Kaiser's image analysis of the variables derived from the transformed coordinates expressing the polymorphism of five *Cephalotes* species. The variables considered are *auricomus* worker, *atratus* minor worker, *atratus* major worker, *pusillus* soldier, *pusillus* worker, *borgmeieri* soldier, *borgmeieri* worker, *angustus* soldier and *angustus* worker. The first two factors together explain 97.7% of the variance observed. Factor 2 divides the variables observed into two groups: *auricomus*, *atratus* minor and *atratus* major workers and all the others. Further explanations in text.

fact, neither visual inspection nor calculation of the relative patristic distances results in a greater morphological similarity between *auricomus* and *atratus* than between one of them and another species considered. A broader analysis including more species from different genera and using grids of different resolution would greatly help the interpretation of the preliminary results on a sample of *Cephalotes* species presented here.

One should not forget, however, that a purely biometric approach to the study of a complex caste system may result in oversimplification and loss of relevant information. Biometry is the ideal instrument to study size variation and, in *Cephalotes*, there are several examples of soldiers and workers overlapping each other in size but differing in morphology.

Since *Cephalotes* soldiers appear to be devoted exclusively to nest defence, there must have been a strong selection pressure in favour of nest defence. There is evidence that behaviourally plastic workers also block the nest entrance with their heads (Delabie, 1994, and our observations reported in this paper) as soldiers do. We are forced to assume that the capacity of workers to perform the same task must

be insufficient to prevent the energetically costly production of an additional caste for this sole purpose. GORDON (1989) emphasises the importance of individuals switching tasks (as *Cephalotes* workers do) as compared to an increased numerical caste distribution in ant societies. In this respect, production of morphologically highly specialised phragmotic soldiers behaviourally less flexible than workers appears as a poorly rewarded option. If, under natural conditions, the requirements of nest defence were much smaller than the potential offered by the actual soldier population, one or more (still unknown) additional tasks must be performed preferentially by phragmotic soldiers.

It is significant in this context, that all soldierless species of *Cephalotes* represent the plesiomorphic condition in our cladogram (Fig. 377, see folding insert), in spite of the uneven presence of soldiers within the genus. No cases of secondary loss of this caste can be demonstrated.

The *Cephalotes* caste system shows another, partly unexpected and still unexplained, phenomenon: the gynes of several species in which the soldiers carry a head disc, also have a cephalic disc.

BARONI URBANI & PASSERA (1996) defined the appearance of the disc among gynes as "probably non-adaptive". One could argue, of course, that the selection pressure for phragmosis may have been exerted first on isolated gynes blocking the entrance of their claustral cell during colony foundation and then had been-transmitted to soldiers. This hypothesis (i. e. the gyne-originated cephalic disc) is supported by ergonomic arguments on caste determination as described by OSTER & WILSON (1978: 101): individual-level selection would render neuters queen-like and not the contrary. Since gynes are the primitive, reproductive caste, "transmission" of the cephalic morphology from gynes to soldiers is also easier to postulate than the reverse phenomenon. This hypothesis is contradicted by the presence of species like *betoi*, *depressus*, *eduarduli* and *borgmeieri* where the soldiers have an incipient disc and the gynes have no disc. In other species like *cristatus* and *pavonii* the soldiers have a completely developed disc and the gynes only an incomplete one. This intuitive ancestrality of the soldier disc is visualised by comparing the cladograms of Fig. 378 (see folding insert) showing that the cephalic disc evolved first in soldiers and only later in gynes.

The cephalic disc of gynes is, however, probably non-functional for another reason: *Cephalotes* species don't dig their nest but use pre-existing wood cavities which are broader than their heads. To block such large nest entrances several individuals must co-operate as neuters actually do, a behaviour obviously impossible for isolated founding queens.

In *Cephalotes*, hence, the following epigenetic and phylogenetic sequences are evident: (1) species with soldiers in which the cephalic disc starts to appear as a round flattening of the frons and with gynes without traces of disk, (2) species with soldiers with completely formed disk and with gynes with a round flattening of the frons only, and, (3) species with soldiers and gynes with complete cephalic disk. These sequences represent a further proof of the direct origin of soldiers from gynes. Information on the epigenetic sequence is available since over 100 years ago, when EMERY (1890, pl. 9, figs. 2c, d) published the figures of the *C. cristatus* soldier with a cephalic disc and of the gyne of the same species without a disc. BARONI URBANI & PASSERA (1996) used this argument to show that gynes repeated the morphological

syndrome of soldiers and not the contrary. Nonetheless, WARD (1997) insists that "the evolution of a polymorphic caste in ants may lead to the larger workers expressing some queen-like traits where this is selectively advantageous, at either the colony level (for example, plug-shaped heads)...". We cannot explain WARD's attitude.

The soldier-selected disc poses another problem: why did gynes also develop a disc? We believe that appearance of a non-functional cephalic disc in gynes of species whose soldiers developed a disc is due to the lack of selection maintaining the primitive gyne morphology. A selection pressure for one phenotype in only one female caste is destined to favour the establishment of the selected phenotype in the selection-free caste as well. A similar argument, i. e. the necessity of multiple, alternative selection pressures in order to maintain phenotypic diversity, has been already developed in general terms by MORAN (1992).

WILSON (1976 b) presents a model in form of a flow-chart to explain the relation between some environmental parameters and the numerous biological oddities of *Cephalotes*. In it, the presence of shield-headed soldiers results from the product of selection pressures due to the interactive competition with other terrestrial and arboreal ants, scavenging behaviour, and arboreal life. As far as we know these same factors apply only in part to the sole other known group of ants with phragmotic soldiers and on which we have some biological information, i. e. *Camponotus* subg. *Colobopsis*, in which scavenging behaviour is unknown.

Another ergonomic argument related to the *Cephalotes* caste system often appearing in the literature is worth discussing here. OSTER & WILSON (1978: 197) state that "the problem of caste multiplication... has certain parallels with the problem of species packing in faunas and floras". WILSON (1968: 56–57) elucidates this point of view by writing that "physical castes are more frequent in tropical ant faunas than in temperate ant faunas" and that "the most specialised castes are found primarily in tropical genera...". "This climatic correlation is consistent with the prediction from ergonomic theory that specialisation in castes already in existence should increase indefinitely until countered by opposite selection pressures imposed by fluctuations in the environment". The same hypothesis is re-proposed in similar words by WILSON (1971: 348 and 1975: 308). The original 1968 paper supports the latitudinal factor in caste proliferation by means of a table in which a list of local faunae world-wide is given together with the percent of "polymorphic species" in each.

At that time, however, true castes (gynes, workers and soldiers) were not considered separately from polymorphic workers. On the other hand, there is no doubt that genera with two neuter castes like *Cephalotes*, *Pheidole*, *Camponotus*, etc. are represented in both temperate and tropical climates, though with many more species in the tropics. A priori, we were inclined to think that the soldier caste originated only once within most ant genera and it is not without surprise that we discovered that our own *Cephalotes* phylogeny implies that the soldiers arose three times independently within this genus (Fig. 377). But we think that there is another, crucial, reason to reject the conclusions drawn from faunal data by WILSON (1968): the fact that in Argentina there are 19 species of *Cephalotes* with a discrete soldier caste and in the United States only 2 is explained much better by the adaptive radiation capacity of a few hypothetical ancestral *Cephalotes* with a soldier caste (actually,

our Fig. 377 shows that the Argentinean and Nearctic species share a unique ancestor with soldiers) than by 19 + 2 separate caste ergonomics arguments after each speciation event. Argentina is simply closer than the United States to the center of maximum *Cephalotes* diversity. Another difficulty with the ergonomic-geographic explanation resides therein that even the existence of a species with soldiers endemic to the tropics does not necessarily imply that the origin of this species (and of its soldiers) must have been in the tropics. We conclude, hence, that the hypothesis of a latitudinal factor in caste specialisation cannot be tested.

There is, however, another explanation for the higher numbers of species with soldiers in the tropics which can be tested by means of information already available: the hypothesis that the variation in the number of species with soldiers at different latitudes may be a simple function of the local faunal diversity, i. e. of the local number of species.

In order to test this hypothesis we used the figures of ant species numbers per biogeographic region published by BOLTON (1995 a). The easiest way to assess the presence of a true soldier caste for a given species relies on the lack or rarity of individuals intermediate between soldiers and workers. For this reason the decision as to the presence or absence of soldiers is very difficult on the basis of limited museum series and we preferred to rely largely on already published information. To count for the number of species with soldiers per biogeographic region we were greatly helped by the catalogue of BOLTON (1995 b) but we have been forced to make some further interpretations and additions which will be explained below.

We have been able to find convincing evidence for the existence of a discrete soldier caste among the following 24 ant genera in the biogeographic regions listed in parentheses:

Acanthomyrmex (Oriental, Malesian). A soldier caste has been considered as being present in all species even when not (yet) described.

Adlerzia (Australian).

Aneuretus (Oriental).

Anisopheidole (Australian)

Azteca (Neotropical). A soldier caste has been considered as being present in all species even when not (yet) described.

Camponotus (Cosmopolitan). A soldier caste has been considered as being present in all species except the members of the subgenus *Myrmoxygenys*, the single *Myrmopytia* and the species of *Karavaievia*. We are aware that this is likely to be an overestimate but for a small order of magnitude only.

Cataglyphis (Palaearctic). Soldiers known only in *bombycinus*.

Cephalotes (Neotropical, Nearctic). Species with soldiers considered as resulting from the present paper.

Cheliomyrmex (Neotropical). A soldier caste has been considered as being present in all species even when not (yet) described.

Cladomyrma (Malesian).

Eciton (Neotropical). A soldier caste has been considered as being present in all species even when not (yet) described.

Gesomyrmex (Oriental, Malesian).

Machomyrma (Australian).

Melophorus (Australian). A soldier caste has been considered as being present in all species even when not (yet) described.

Monomorium (Cosmopolitan). The species with soldiers resulting from BOLTON (1995 b) are: *armstrongi* (Australia), *criniceps* (India) and *scabriceps* (India). To these species with

formally described soldiers it has been added *dentigerum* (Middle East) as reported by BARONI URBANI & AKTAÇ (1981).

Myrmecorhynchus (Australian). A soldier caste has been considered as being present in all species even when not (yet) described.

Notostigma (Australian).

Oligomyrmex (Cosmopolitan except Nearctic). A soldier caste has been considered as being present in all species even when not (yet) described.

Perissomyrmex (Oriental, Neotropical). A soldier has been recently described by LONGINO & HARTLEY (1994) for *snyderi* (Mexico).

Pheidole (Cosmopolitan). A soldier caste has been considered as being present in all species even when not (yet) described. We are aware that this is likely to be an overestimate but for a small order of magnitude only.

Pheidologeton (Oriental, Malesian, Australian, Afrotropical). A soldier caste has been considered as being present in all species even when not (yet) described.

Philidris (Oriental, Malesian, Australian). In the description of this genus, SHATTUCK (1992) states that the workers are "polymorphic, majors with ocelli", a frequent soldier character. In another passage he adds that workers are "less commonly monomorphic". From the literature we have been able to find evidence for the presence of soldiers among the following taxa: *butteli* (FOREL) (unavailable name, quadrinomen) from Sumatra (evidence of soldiers: FOREL, 1913 a); *cordata* (SMITH) from Indonesia (evidence of soldiers: KARAWAJEW, 1926); *jactans* (FOREL) (unavailable name, quadrinomen; referred to *laevigata* (Emery) by VIEHMEYER, 1916) from Singapore (evidence of soldiers: FOREL, 1911 c).

Pseudolasius (Oriental, Malesian, Australian, Afrotropical). A soldier caste has been considered as being present in all species even when not (yet) described.

Solenopsis (Cosmopolitan). The species with soldiers resulting from BOLTON (1995 b) are: *caffra* (South Africa, soldier described for its synonym *cyclops*), *clarki* (Australia), *egregia* (Argentina), *geminata* (Central America, soldier described for its synonym *cephalotes*), *gensterblumi* (Brazil, soldier described for its synonym *prevalens*), *photophila* (Argentina), *xyloni* (U. S. A.).

Since fragments of the postembryonic development of castes are known for only one of these genera (*Pheidole*), the list will obviously be corrected in the future. In particular, our omission of some species of *Monomorium* from the list is due only to our inability to make a decision given the scanty material we have been able to see and on the information in the literature.

From the above one can compare the number of species with soldiers with the total number of species reported from each biogeographic region.

There seems to be a plausible relation between the number of species with soldiers and the local faunal diversity (Fig. 379). From the regression equation given in the figure it appears that ca. 79% of the variability observed in the number of species with soldiers per biogeographic region is explained by the corresponding local species diversity.

A final problem is worth discussing in connection with the caste system of *Cephalotes*. WHEELER (1984), from a comparative behavioural study, suggested that the primitive cephalotine caste could be the soldier caste and that workers may have appeared later, a hypothesis considered as biologically improbable by BARONI URBANI & PASSERA (1996). Now, in the pages above, we have shown that the workers of the soldierless species *auricomus* are much more similar to gynes than the workers of species with both neuter castes. *Auricomus* workers, being more similar to gynes than other workers of the same genus, may be regarded as a kind of soldiers (the usually gyne-like caste), a fact previously unknown, and which appears to

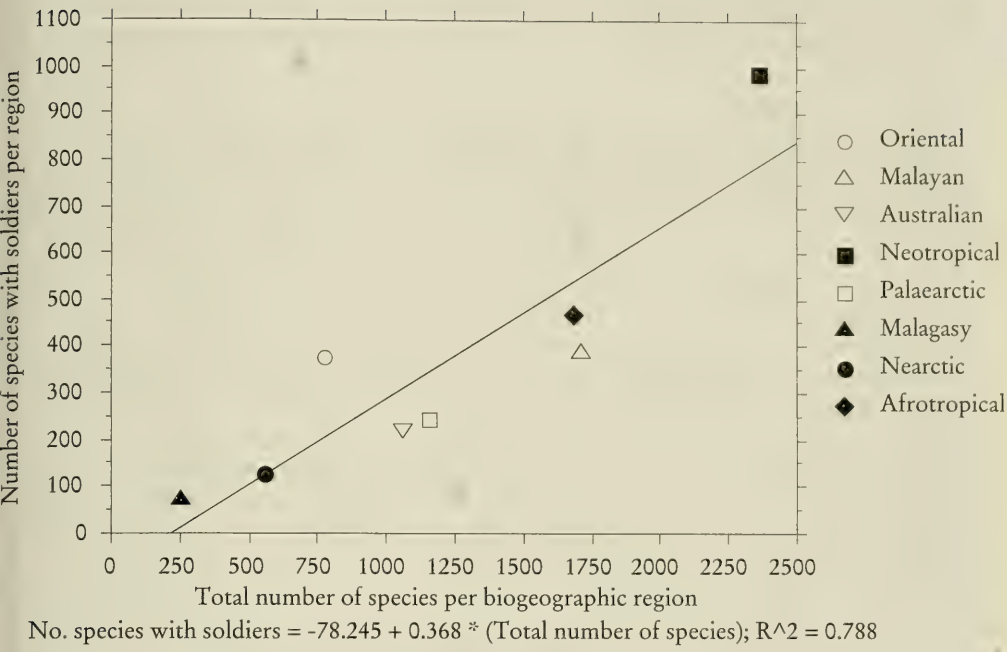

Fig. 379. Scattergram of the number of known species of ants per biogeographic region compared with the number of ant species with a soldier caste. Further explanations in text.

support WHEELER's hypothesis. A great morphological similarity between gynes and neuters should be expected for the plesiomorphic caste and this worker-gyne similarity is known to exist in a number of ant genera having only one neuter caste (e. g. most members of the subfamily Ponerinae, *Myrmica*, *Formica*, and many others). Moreover, one may easily imagine that the morphologically gyne-like plesiomorphic caste should have been behaviourally worker-like. In this case only the later production of gyne-unlike "true workers" allowed narrowing of the behavioural repertoire and specialisation of "true soldiers".

The presumed ancestral status of either workers or soldiers cannot be decided on the basis of our *Cephalotes* phylogeny: the number of evolutionary steps necessary to add the second caste remains the same whether the first caste is called soldier or worker. We can suggest no logical way to decide on one alternative or the other, if the discussion is restricted to *Cephalotes*. The same is not true if we broaden the analysis to the whole of the Formicidae. Assuming that the selection of gyne-similar soldiers always happened first and the appearance of gyne-dissimilar workers followed, a number of additional steps are required to explain the secondary loss of soldiers in several ant genera in which only one gyne-dissimilar caste is known (e. g. *Carebara*, *Diplorhoptrum*, *Tetramorium*, *Crematogaster*, *Leptanilla*, *Lasius*, etc.). Alternatively, a different mechanism of caste evolution should be assumed for these genera.

We supposed that hypothetically ancestral soldiers, if they ever existed, should have had a worker-like behaviour. If this assumption is true, the problem is restricted chiefly to a matter of semantics.

6.5. Teratology

A large proportion of the workers (29%) and of the worker pupae (19%) of a *C. atratus* colony from Trinidad described by WEBER (1957) were ergatandromorphs (i. e. with a basic worker morphology and some male characters or even male genitalia) and/or with clearly teratologic ram's horn antennae (figured by WHEELER, 1936 a: 187). According to WEBER (l. c.) these anomalous workers oriented themselves, carried food, and behaved like other normal workers. WHEELER (1910, fig. 102) illustrates a soldier of *C. bimaculatus* (cited as *aztecus*) with mesothoracic vestigial wings. SANTSCHI (1921 b) described the new species *C. fossithorax* for its peculiar mesosomal morphology which, afterwards, was revealed to be a probable intercaste syndrome (KEMPF, 1958 a).

We also observed – among the *Cephalotes* material we examined – several malformations different in nature and greater in extent than in other ants. We encountered many more teratologic individuals during our work on *Cephalotes* than in all of our remaining myrmecological studies.

Among the most significant ones we record:

C. atratus, a worker with abnormal head, very short and convex.

C. auricomus, workers with asymmetric petiolar spines or without them.

C. auricomus, a dwarf worker with very long petiolar spines.

C. biguttatus, a worker with fused petiole and postpetiole.

C. clypeatus, an ergatandromorph, essentially worker with half a male head.

C. depressus, a dwarf gyne, ca. 15–20 % smaller in all body parts than the other known gynes.

C. kukulcan, a worker without the membranaceous border of the propodeum and with a strongly asymmetric petiole (normally lamellate on the left side and with a minute denticle on the right one).

C. laminatus, a worker with asymmetric coloured spots on the frontal carinae.

C. marginatus, a worker with a normal head dorsally up to the frontal carinae and male morphology below the carinae.

C. pallens, a male with only the right side of the petiole, fused with the postpetiole.

C. pallidicephalus, two workers with a normal lamellate petiole and postpetiole on the left side but without lamellae on the right side.

C. pavonii, a soldier with the first gastral sternite longitudinally fissured in the middle.

C. pusillus, a worker without petiole and postpetiole (i. e. with the gaster articulated to the propodeum).

C. pusillus, a worker with aberrant, very broad, gaster.

C. pusillus, a worker with a pair of symmetric holes on the frontal carinae.

C. pusillus, a soldier with a pair of symmetric holes on the frontal carinae.

C. pusillus, a worker with the left middle leg yellow (rest of the body normally black) and with two consecutive articulations (only one functional) between femur and tibia.

C. pusillus, a worker with only one pair of legs (this specimen survived for several weeks in the lab, though it was unable to walk and was carried by other individuals).

C. pusillus, a giant soldier with mesothoracic, sclerified wing vestiges.

C. targionii, two dwarf gynes ca. 20% smaller than normal gynes from the same colony.

C. targionii, a male with a second, lateral, anal opening.

C. varians, a soldier with postpetiole broadly lobed on one side and simply pointed on the other one.

It would be useless describing and commenting further in detail on all these malformations, but the point we would like to make is that the morphology of at least some of the abnormal individuals reported above can be better explained genetically than in other ways. The (plausible) alternative explanation suggested by WHITING (1938) for other, similar ant mosaics to be interpreted as cephalic intersexes does not apply to all the cases reported here since a number of *Cephalotes* mosaic morphologies affect the pedicel and the gaster. All together the abnormal individuals we listed above suggest a spontaneous somatic mutation rate much greater in *Cephalotes* than in other ants known so far.

6.6. Relationships with other arthropods

Ants of the genus *Cephalotes* are likely to represent a very successful evolutionary model. According to HESPENHEIDE (1986), 13 out of 21 Central American species of "*Zacryptocerus*" known at that time appear to be models for Batesian mimicry by no less than 40 different species of arthropods (particularly buprestid beetles). Some *Cephalotes* mimics, however, are specialised predators of their model. In Brazil Aphantochilid spiders imitate species of *Cephalotes* and eat them. Another Brazilian thomisid spider, *Bucranium*, does not resemble *Cephalotes* but can eat them just the same (BRISTOWE, 1925 and 1941). The same behaviour probably referring to the same genera had been already described by HINGSTON (1927) in Guyana. *Aphantochilus rogersi* is known in two morphs, a large morph imitating the large *C. atratus* and a small morph (described as *Cryptoceroides cryptocerophagus* by DE PIZA, 1937) imitating the small *C. pusillus*. The spider mimic is likely to gain some Batesian protection from resembling the ant (REISKIND, 1971) but it appears also to be a specialised predator of *Cephalotes* since – under laboratory conditions – it attacks and consumes species of this genus but it refuses ants of the genus *Camponotus* and *Drosophila* flies (OLIVEIRA & SAZIMA, 1984; OLIVEIRA, 1986). CRAWLEY (1916) lists five species of Coccidae associated with *C. minutus* and *C. atratus* in Guyana. Even more astonishing is the strict association between the membracid *Tragopa peruviana* and *C. atratus* as reported by RICHTER (1945) in Colombia. This author has been able to observe *T. peruviana* without ants only once and the individuals of this antless population were marked by white spots instead of being regularly black as are all the populations living in strict association with the equally black *Cephalotes* (but see also CORN, 1976). LETURNEAU & CHOE (1987) describe frequent associations between planthoppers and membracids on one side, and *C. porrasi* on the other, in a tropical wet forest of Costa Rica but consider the association of the ant with both homopterans as purely opportunistic. By contrast, in the Brazilian state of Maranhão, *C. placidus* is listed by BARTOSZECK (1980) as being among the natural enemies of the pest aphid *Toxoptera citricida*, the vector of the virus producing the "tristeza" of the citrus; this statement, however, appears to be inferred essentially from the fact that the ant and the aphid have been recorded simultaneously from several branch samples. In cacao plantations in Venezuela, JAFFE et al. (1986) demonstrated a negative correlation between the presence of *C. atratus* and the pest cerambycid beetle *Steirastoma breve*.

The only information we have been able to obtain about true or presumed myrmecophilous arthropods living in *Cephalotes* nests stem from EIDMANN (1936) who reports collecting a larva of *Microdon* (Diptera, Syrphidae), the pseudoscorpion

Pycnochernes brevifemoratus, and a diplopod in a nest of *C. pusillus* in the state of Rio de Janeiro.

Colonies of *C. varians* experimentally introduced onto mangrove "islands" of the Florida keys established easily, provided the mangrove ant fauna contained neither *Crematogaster* nor *Xenomyrmex* (COLE, 1983 a). On the other hand, according to FOWLER et al. (1994), native *Cephalotes* species in Brazil disappear entirely from areas colonised by the introduced pantropical ant *Pheidole megacephala.*

WHEELER (1901 a, b) reports frequent parabiotic associations between *C. bimaculatus* (cited as *aztecus*) and *Crematogaster brevispinosa* MAYR. Not only were the two ant species often found together under natural conditions in Mexico, but, transported to the laboratory in Texas, they shared the same artificial nest without showing any aggression or avoidance behaviour. BRUCH (1923) cites as frequent a similar association between *C. fiebrigi* (cited as *guttifer*) and *Crematogaster brevispinosa malevolens* in Argentina. ADAMS (1990) describes a statistically significant association between *C. maculatus* and the arboreal dolichoderine ant *Azteca trigona* in the mangrove forests on the Atlantic coast of Panama: he interpreted this association as a case of "information parasitism" in which *Cephalotes* exploits the foraging trails traced by *Azteca* to have easier access to food sources.

LESTON (1978) describes *C. atratus* in the Brazilian state of Bahia as occupying large portions of secondary forest with high population densities spatially superimposed onto a small species of *Crematogaster*. He interpreted this situation as the sole known exception to his "ant mosaic theory" for which numerically dominant ant species should be also mutually exclusive of other ants.

RETTENMEYER (1963) reports that the driver ants *Eciton burchelli* are "quicker to attack and more pugnacious, and they have a stronger bite and a more potent sting (to a person) than any other species of *Eciton*. ... I have seen mammals like the tapir (*Tapirella bairdii*), anteater (*Tamandua tetradactyla*), and coati (*Nasua narica*) being driven out of areas where they were feeding by swarm raids of *burchelli*. ... Other ants, such as species of *Atta* and *Cryptocerus* [= *Cephalotes*], either were not attacked, or they resisted strongly and were rarely killed even though they are smaller than the *Eciton*".

According to ZENNER-POLANIA (1990), "*Zacryptocerus*" sp., by nesting in hollow twigs of *Inga* spp., is one of the few indigenous ant species apt to coexist with the imported pest ant *Paratrechina fulva*. In another paper (ZENNER DE POLONÍA & RUIZ BOLAÑOS, 1985), however, it is stated that "*Zacryptocerus* sp." coexist with *P. fulva*, but are displaced by the introduced *Paratrechina*.

There are several reports of *Cephalotes* spp. coexisting peacefully in different nests on the same tree with other ants. One of us (MLDA) observed in the town of Lins (S. Paulo, Brazil) up to three different *Cephalotes* species (*clypeatus*, *pallidoides* and *borgmeieri*) nesting in different branches of the same tree. At least in *C. clypeatus* and *C. borgmeieri,* individuals of the same species transported close to the nest entrance from a different nest are regularly attacked by the nest occupants, even when the two original nests were only a few meters distant from each other. In the laboratory small groups (2–3 workers) of *C. borgmeieri* and *C. clypeatus* from different colonies from the same locality start aggressing cospecific allocolonial individuals only minutes after their introduction in a Petri dish.

6.7. Mortality factors and survival strategies

If the demographic and radiative success of *Cephalotes* is likely to be correlated with its nesting habits and feeding behaviour (see above), the advantages derived from these factors must be maintained by a reduction of the mortality rate. In the following we summarise the information available on *Cephalotes* diseases, predators and defence mechanisms.

6.7.1. Diseases

One of us (MLDA) collected a *C. minutus* worker in Manaus with an abnormally distended gaster. The ant was inside the nest and moved slowly because of the size of the gaster. Immediately after fixation in alcohol the gaster exploded revealing a very large juvenile mermithid nematode (Fig. 380) probably belonging to an undescribed genus (information on the nematode courtesy of Dr. G. O. POINAR, Jr.). The ant worker showed no external malformations as is the case for other known examples of nematode parasitism in ants (see e. g. WHEELER, 1928, and POINAR, 1983). This is the first record of Mermithidae from ants in the tropics. The record of a mermithid in *Cephalotes* is unexpected for two reasons: 1) One would expect that the pollen filtering proventriculus of *Cephalotes* would also be able to filter a nematode cyst. 2) Ants usually ingest the nematodes as cysts (POINAR, 1983), an improbable occurrence if the pollen diet we emphasise in this paper is assumed to be the main food source for *minutus*. It is more likely that the cyst had been ingested while the *minutus* worker was feeding on carrion or on dead invertebrates. Dr. POINAR suggests that the nematode may have emerged from its cyst in the crop of the ant and penetrated the body cavity in this way.

In Ecuador BROWN (1997) discovered two species of phorid flies parasitising *C. atratus*: one is an ant-decapitating species of the genus *Apocephalus*, and the other, a species of *Diocophora*, parasitises its legs.

In the Brazilian state of Pará *C. atratus* can be infested by epizootic pathogenic fungi of the genus *Cordyceps* (Laboulbeniales, Ascomycotina). The most common species (*C. kniphofioides*) can also be found – with different varieties – on other ant species, though *C. atratus* is the most heavily infested one. According to EVANS & SAMSON (1982) ants infected by the pathogen clean themselves very often and search for a shelter in tree bark where they die. On discovering the dead bodies, other *Cephalotes* workers tend to remove them from the tree by dropping them to the tree base. As already stressed by EVANS (1982), this auto-seclusion behaviour – already described for other ants infested by entomogenous fungi – appears to assume unique features in *Cephalotes*: the diseased ants from large areas tend to move to the same tree where they eventually die. This "cemetery tree" is usually in the centre of the local epizootic but distant from ant nests or from ant trails. EVANS & SAMSON (1982) collected 2,376 dead *C. atratus* workers with mature *Cordyceps* stromata from a single "cemetery tree" in two years. OI & PEREIRA (1993) suggest that the allo-grooming of infested individuals (unreported for *C. atratus*) might contribute to the intra-colony dissemination of *Cordyceps*.

Fig. 380. *Cephalotes minutus* (FABRICIUS), worker from Manaus parasitised by a mermithid nematode. Explosion of the gaster with the consequent display of the nematode is an artifact resulted from fixation of the specimen in alcohol.

6.7.2. Predators

There are relatively meagre records of *Cephalotes* being preyed on by other animals, if one considers the commonness and the density of some of its species. Actually, no Cephalotini are listed as vertebrate or invertebrate prey by BEQUAERT (1922 a) and there are a few records of primates feeding on *Cephalotes*. One of the commonest species of the genus, *C. atratus*, is preyed on by the saki monkey, *Pithecia hirsuta* (HEYMANN & BARTECKI, 1990) and by the capuchin monkey, *Cebus capucinus* (ROBINSON, 1986). In the central Amazon, *Cephalotes* spp. represent 11.7% of the individual insects and 38.7% of the volume of recognisable insect remains in the faeces of the small, nocturnal, silky anteater (*Cyclopes didactylus*) (BEST & HARADA, 1985). Under the locality records we give for *C. pusillus*, however, we report 6 soldiers of this species as issuing from the stomach of a *Tamandua tetradactyla*. The fact that the sample consisted only of soldiers, a caste virtually never venturing outside the nest, strongly suggests that the anteater must have opened a *C. pusillus* nest. CRUZ & JOHNSTON (1979) record the presence of "*Paracryptocerus*" in the stomach of the common flicker (*Colaptes auratus gundlachi*), a bird foraging primarily by pecking on forest trees on Gran Cayman

Island. WEBER (1957) states that the stomachs of ant-eaters collected close to *Cephalotes* nests in Trinidad contained no representatives of this genus although occasionally workers foraging on the ground can be eaten by the giant toad *Bufo marinus* (WEBER, 1938). Lizards of the genera *Mabuya* and *Anolis* eat *Cephalotes* only occasionally (CORN, 1976). ZEH & ZEH (1990) describe how *C. atratus* workers are regularly preyed on by the subsocial pseudoscorpion *Paratemnus elongatus* in Panama. It is unlikely, however, that the natural density of this predator may affect the *Cephalotes* population in a significant way. We already mentioned (in Chapter 6.6) the fact that *Cephalotes* spp. are the obligatory prey of spiders of the genus *Aphantochilus* (OLIVEIRA & SAZIMA, 1984). OLIVEIRA & SAZIMA (l. c.), however, add that they have "found no evidence... about any spider, other than aphantochilids, preying upon cephalotine ants".

6.7.3. Defence mechanisms

POHL & KOLLAR (1832) list *Formica caustica* (= *Cephalotes minutus* or a closely related species) among the 15 most annoying Brazilian "insects" together with fleas, scorpions, mosquitos, etc. In their description of the effectiveness of this ant they notice correctly that it bites and does not sting and they give also the first account of *Cephalotes* defence pheromones as: "Ihr Biss ist minder schmerzhaft, als der brennende Saft, den sie von sich gibt, und der einen nesselartigen Ausschlag auf einige Stunden bewirkt".

Several species of *Cephalotes* react to disturbance by immobilising themselves after first folding their appendages under the characteristic lateral expansions of their body.

COYLE (1966) described other *Cephalotes* species, that, instead of the above "turtle strategy", raise their gaster perpendicularly to the major body axis while emitting a volatile defensive substance from the apex of the abdomen. These observations, based on three species observed in Costa Rica, allowed an important morphological correlate of the defence strategy to be recognised: species adopting the "turtle strategy" have much steeper posterior propodeal and anterior petiolar faces which make an angle of ca. 35° with the body in the resting position; species exhibiting the "aerosol strategy" have much more flattened propodea and petioles which make an angle >110° with the body in resting position. KEMPF (1951: 157) uses the shape of the propodeum and of the petiole to separate his "*pavonii*-group" from the other species of the genus in his key to the identification of the species of "*Paracryptocerus*". One could speculate that the species separated in the first two couplets of the key correspond respectively to those adopting the "turtle strategy" or the "aerosol strategy".

The sole exocrine secretions identified from cephalotine ants so far are a ketone (4-heptanone) and an alcohol (4-heptanol) synthesised in the mandibular glands of *C. varians*. Both compounds function as alarm pheromones eliciting either an escape reaction or immobilisation in the "turtle" posture (OLUBAJO et al., 1980). The histology of the gland producing these compounds has been described by GAMA & DA CRUZ-LANDIM (1982).

Some *Cephalotes* species are black, or brown or dull coloured. This probably functions in evading detection by offering a general resemblance to the environment. The female castes of many other species bear one or more pairs of coloured spots on different body parts (Tab. 6). *Cephalotes* males are always dull coloured and

Tab. 6.1. Distribution of coloured patterns among workers, soldiers and gynes of *Cephalotes*. Species *adolphi* to *inaequalis*. Most of the colours tabulated are likely to have a mimetic function but a few of them may be interpreted as aposematic.

	Body colour	Worker: No. of coloured spots			Soldier: No. of coloured spots			Gyne: No. of coloured spots		
		Head	Mesosoma	Gaster	Head	Mesosoma	Gaster	Head	Mesosoma	Gaster
adolphi	light brown	4 yellowish	0	1 yellowish	?	?	?	?	?	?
alfaroi	black	2 dark orange	0	2 lighter	2 lighter	0	2 lighter	?	?	?
angustus	black	2-4 yellow	0	2 orange	1-2 yellow-orange	0-2 orange	2-4 orange	1-2 orange	0-2 orange	2-4 orange
argentiventris	black	2 orange	0	metallic reflexes	—	—	—	?	?	?
atratus	black	2 lighter	0	2 brown	—	—	—	0	0	0
auriger	black	2 yellow	0	2 yellow	?	?	?	?	?	?
auricomus	silvery reflexes	2 reddish	0	2 reddish	—	—	—	2 dark brown	0	0
basalis	black	0-2 dark brown	0-2 reddish	0	0	0	2 silvery	0	0	2 orange
betoi	black	2 orange	2 orange	2 yellow	2 brown	0	0	0	0	0
biguttatus	black	2-4 orange	4 orange	2 orange	2 dark orange	4 dark orange	2 dark orange	2 dark orange	0	2 yellow
bimaculatus	black	2 orange	0	2 orange	2 yellow	0	2 orange	2 yellow	0	2 orange
bivestitus	black	2 yellow	0	0	1 yellow	3 yellow	4 yellow	2 yellow	1-2 yellow	4 yellow
bohlsi	black	2 yellow	0	0	2 yellow	0	0	?	?	?
borgmeieri	black	0-2 lighter	2 lighter	0	0-2 lighter	0	0	0-2 lighter	0	0
bruchi	black	2 brown	0	0	1-2 reddish	1 yellow	0	2 orange	0	1 lighter
chacmul	black	2 yellow	0	2 yellow	2 lighter	0	2 yellow	?	?	?
christopherseni	black	4 orange	0	2 orange	2 reddish	0	0-2 reddish	2 lighter	0	2 lighter
clypeatus	yellow	4 yellowish	2 yellowish	1 yellowish	4 yellowish	2 yellowish	1 lighter	2 lighter	0	4 white "eyes"
coffeae	black	2 yellow	0	2 yellow	2 lighter	0	2 orange	2 dark orange	0	4 yellow
columbicus	black	2-4 reddish	0	0-2 lighter	2 reddish	0	2 lighter	2 lighter	0	0-4 lighter
complanatus	black	0-2 lighter	2 lighter	2 lighter	0	0	2 silvery	0	0	2 dark orange
conspersus	black	2-4 yellow	0	3 black	1 orange	0	4 yellow	?	?	?
cordatus	black	2-4 yellow	2 orange	2 orange	2 lighter	0	2 lighter	2 lighter	0	0
cordiae	black	0	0	0	0	0	0	2 lighter	0	2 yellow
cordiventris	black	0	0-2 lighter	0-2 lighter	0	0	2 silvery	0	0	2 white
crenaticeps	black	2 yellow	0	2 yellow	2 lighter	0	2 orange	2 lighter	0	2 orange
cristatus	black	2 brown	0	0-2 lighter	2 lighter	0	0	2 reddish	0	0
curvistriatus	black	2 yellow	0	2 yellow	2 orange	0	2 orange	2 orange	0	2 orange
decolor	black	0-2 lighter	2 lighter	0-2 lighter	0	0	entirely reddish	0	0	reddish
decoloratus	dark brown	2 lighter	2 lighter	2 lighter	0	0	lighter	?	?	?
dentidorsum	brown	4 lighter	0	2 lighter	?	?	?	?	?	?
depressus	black	2 lighter	0	0-2 lighter	2 lighter	0	0	2 lighter	0	0
duckei	dark brown	4 yellow	4 yellow	2 yellow	2 reddish	4 reddish	reddish, 1 lighter	2 lighter	0	4 orange
ecuadorialis	black	4 orange	0	2 orange	?	?	?	2 lighter	0	4 orange
eduarduli	black	2 orange	0	0	1-2 lighter	0	0	1-2 lighter	0	0
emeryi	black	0	0	0	?	?	?	?	?	?
femoralis	black	2 reddish	2 reddish	0	?	?	?	?	?	?
fiebrigi	black	2 yellow	0	0	2 lighter	2 yellow	2-4 yellow	2 yellow	2 yellow	4 yellow
flavigaster	black	2 reddish	0	entirely orange	—	—	—	?	?	?
foliaceus	brown	4 yellow	2 yellow	1-3 yellow	2 lighter	2 lighter	?	?	?	?
fossithorax	black	2 lighter	0	entirely lighter	2 lighter	2 orange	0	2 lighter	2 lighter	2-4 yellow
frigidus	black	2 yellow	2 yellow	1 yellow	1 yellow	1 brown	4 yellow	1 yellow	1 brown	4 yellow
goeldii	black	4 yellow	0	2 yellow	1 yellow	2 yellow	2 yellow	1 yellow	2 yellow	4 yellow
goniodontus	black	2 orange	4 yellow	2 yellow	2 orange	4 yellow	2 yellow	?	?	?
grandinosus	light brown	4 lighter	4 lighter	2 lighter	0	4 lighter	2 lighter	4 lighter	0	1-2 brown
guayaki	black	2 yellow	0	0	2 brown	2 brown	4 yellow	2 brown	2 brown	4 yellow
hamulus	black	2 brown	0	2 brown	—	—	—	2 brown	0	?
hirsutus	silvery reflexes	2 orange	0	1 yellow	?	?	?	?	?	?
inaequalis	black	4 orange	10 orange	2 yellowish	2 brown	0	2 yellowish	2 brown	0	4 orange

Tab. 6.2. Distribution of coloured patterns among workers, soldiers and gynes of *Cephalotes*. Species *inca* to *setulifer*. Most of the colours tabulated are likely to have a mimetic function but a few of them may be interpreted as aposematic.

	Body colour	Worker: No. of coloured spots			Soldier: No. of coloured spots			Gyne: No. of coloured spots		
		Head	Mesosoma	Gaster	Head	Mesosoma	Gaster	Head	Mesosoma	Gaster
inca	part. silvery reflexes	0	0	2 golden	?	?	?	0	0	2 golden
incertus	light brown	2 lighter	4 lighter	2 lighter	2 lighter	4 lighter	4 lighter	2 lighter	2 lighter	4 lighter
insularis	black	2 yellowish	0	1-3 orange	2 reddish	0	0	2 reddish	0	0
jamaicensis	brown	2 lighter	0	0	0	0	0	?	?	?
jheringi	brown to black	2 orange	0	0	1 orange, 2 lighter	1-2 orange	0-2 yellow	2 yellow	2 yellow	0-4 yellow
klugi	black and yellow	?	?	?	?	?	?	1 yellow, 2 lighter	3 yellow	yellow, 1 black stripe
kukulcan	black	4 yellow	4 yellow	2 yellow	1 orange, 1 black	3 orange	yellow, 1 black	orange border	1-2 yellow	4 yellow
laminatus	black	4 yellow	8 yellow	2 transparent	0-2 brown	0	0-4 yellowish	0-2 brown	0	4 orange
lanuginosus	black	2 orange	0	0	1 orange, 2 lighter	2-3 orange	0-4 yellow	1 orange, 2 lighter	2 orange	4 yellow
lenca	black	2 yellow	0	2 yellow	?	?	?	?	?	?
liepini	brown	2 lighter	4 lighter	2 lighter	0	2 lighter	1 brown	?	?	?
liogaster	black	2 yellowish	0	0	1 orange	1 orange	0-4 yellow	1 orange, 2 lighter	1 yellow	4 yellow
maculatus	dark brown	2 lighter	4 lighter	2 yellow	0	0	1-4 orange	0	0	4 orange
manni	black	2 lighter	0	0	2 reddish	0	0	?	?	?
marginatus	black	2 reddish	0	0	—	—	—	0	0	0
membranaceus	light brown	4 lighter	4 lighter	lighter border	2 lighter	2 lighter	5 yellowish	2 lighter	0	4 yellowish
minutus	black	2-4 yellow	0	2 yellowish	2 reddish	0	1-4 orange	2 reddish	0	2-4 orange
mompox	black	0	0-2 lighter	0-2 lighter	?	?	?	?	?	?
multispinosus	black	2-4 orange	4 yellow	2 yellow	2 orange	4 orange	2 orange	2 reddish	0	2 orange
nilpiei	dark brown	2 orange	4 orange	2 orange	2 orange	4 orange	4 orange	?	?	?
notatus	black	2 yellow	0	1-2 yellow	1 yellow, 1 black	4 yellow	1-3 yellow	1 yellow, 1 black	4 yellow	4 yellow
oculatus	black	0	0	0	—	—	—	0	0	0
opacus	black	0	0	0	0	0	0	0	0	0
pallens	reddish	0	0	0	0	0	0	0	0	0
pallidicephalus	black	2 yellow	0	2 yellow	1 yellow	4-6 orange	1-4 yellow	1 orange	2 orange	4 orange
pallidoides	brown	0	0	0	0	0	0	0	0	0
pallidus	dark brown	0	0	0	0	0	0	0	0	0
palta	black	2 orange	0	0	1 yellow, 1 black	2 yellow	4 yellow	?	?	?
palustris	black	4 yellowish	10 yellowish	2 yellowish	2 brown	0	0	?	?	?
patei	brown	2 lighter	0	0	2 lighter	0	0	2 lighter	0	0
patellaris	brown	2 lighter	0	0	0	0	0	0	0	0
pavonii	black	2 brown	8 yellow	2 brown	2 lighter	0	0	2 lighter	0	0
pellans	brown	0	0	0	0	0	0	0	0	0
persimilis	light brown	2 yellowish	4 yellowish	2 yellowish	0	0	0	2 lighter	0	1-2 darker
persimplex	light brown	2 lighter	4 lighter	2 lighter	2 lighter	0	0	2 lighter	0	2 darker
peruviensis	dark brown	4 lighter	0	2 lighter	?	?	?	?	?	?
pileini	brown	2 yellowish	4 yellowish	2 yellowish	2 lighter	4 yellowish	2 yellowish	2 lighter	4 lighter	4 lighter
pilosus	black	2 orange	0	0	2 orange	2 orange	0-4 orange	2 orange	0	0-4 yellow
pinelii	dark brown	2-4 orange	4 yellow	2 yellow	2 lighter	4 lighter	1-4 orange	2 lighter	4 lighter	4 yellow
placidus	black	0	0	0	—	—	—	0	0	0
porrasi	black	0	0	0	0	0	0	0	0	0
prodigiosus	?	?	?	?	1 orange	2 orange	0	1 orange, 2 lighter	3 orange	4 orange
pusillus	black	2 brown	0	0	2 lighter	0	0	2 lighter	0	0
quadratus	light brown	2 lighter	0	0	2 lighter	2 lighter	4 orange	?	?	?
ramiphilus	black	0	0	0	0	0	0	0	0	
resinae	black	2 lighter	0	0	—	—	—	?	?	?
robweri	black	2 lighter	0	0	0-2 lighter	0	0	0	0	0
scutulatus	black	4 yellow	4 yellow	1-2 yellow	1 orange	3 yellow	1-4 yellow	1 yellow, 1 black	1 yellow	4 yellow
serraticeps	black	2 lighter	0	0	0	0	0	0	0	0
setulifer	black	2 brown	0	2 brown	0	0	2 yellow	0	0	2 yellow

Tab. 6.3. Distribution of coloured patterns among workers, soldiers and gynes of *Cephalotes*. Species *simillimus* to † *ventriosus*. Most of the colours tabulated are likely to have a mimetic function but a few of them may be interpreted as aposematic.

	Body colour	Worker: No. of coloured spots			Soldier: No. of coloured spots			Gyne: No. of coloured spots		
		Head	Mesosoma	Gaster	Head	Mesosoma	Gaster	Head	Mesosoma	Gaster
simillimus	black	2 orange	0	0	2 lighter	0	0	?	?	?
sobrius	black	2 yellow	0	2 yellow	2 reddish	0	2 orange	2 brown	0	2 yellow
solidus	black	2 lighter	0	0	?	?	?	?	?	?
spinosus	black	4 yellow	8 orange	2 yellow	2 reddish	0	2 yellow	2 reddish	0	4 yellow
supercilii	dark brown	2 orange	0	0	2 yellowish	2 orange	0	2 yellowish	2 orange	2 orange
taino	black	2 lighter	0	0	—	—	—	?	?	?
targionii	black	2 yellow	0-2 yellow	0-2 yellow	1 yellow, 1 black	2 orange	2-4 orange	1 yellow, 1 black	2 orange	4 yellow
texanus	black	2 orange	0	2 yellow	2 orange	2 orange	2 yellow	2 orange	0	2 yellow
toltecus	black	2 brown	0	0	2 reddish	0	0	?	?	?
trichophorus	black	2 brown	0	2 lighter	?	?	?	?	?	?
umbraculatus	yellow to brown	4 yellowish	2 yellowish	4 lighter	2 lighter	0	4 lighter	2 lighter	0	1-2 darker
unimaculatus	black	2 orange	0	1 orange	—	—	—	?	?	?
ustus	black	4 yellowish	4 yellowish	1 yellow	4 lighter	4 lighter	1 yellow	?	?	?
varians	brown	0	0	0	0	0	0	0	0	0
vinosus	black	2 orange	0	entirely reddish	—	—	—	?	?	?
wheeleri	black	2 yellowish	0	0	2 reddish	0	0	?	?	?
†*alveolatus*	black	2 lighter	0	0	?	?	?	?	?	?
†*bloosi*	black	2 lighter	0	0	?	?	?	?	?	?
†*brevispineus*	black	2 lighter	0	0	?	?	?	?	?	?
†*caribicus*	black	2 lighter	4 lighter	0	?	?	?	?	?	?
†*dieteri*	black	2 lighter	0	0	?	?	?	?	?	?
†*hispaniolicus*	black	2 lighter	2 lighter	0	?	?	?	?	?	?
†*integerrimus*	black	2 lighter	0	0	?	?	?	?	?	?
†*jansei*	black	0	0	0	?	?	?	?	?	?
†*maya*	black	2 lighter	4 lighter	0	?	?	?	?	?	?
†*obscurus*	black	2 lighter	0	0	?	?	?	?	?	?
†*olmecus*	black	2 lighter	4 lighter	2 lighter	2 lighter	4 lighter	?	?	?	?
†*poinari*	black	4 lighter	4 lighter	0	?	?	?	?	?	?
†*serratus*	black	0-2 lighter	0	0	?	?	?	?	?	?
†*squamosus*	black	2-4 lighter	0-2 lighter	0	?	?	?	?	?	?
†*sucinus*	brown	4 lighter	2 lighter	2 lighter, 1 black	?	?	?	?	?	?
†*ventriosus*	black	2 lighter	2 lighter	0	?	?	?	?	?	?

don't differ chromatically from what one would expect from an average ant. In some instances a morphological character often cursorily mentioned in the literature on *Cephalotes*, namely the "canaliculate hairs" (Fig. 381) and present only in the female castes of some species, may have an analogous, unusual chromatic effect. These hairs have a concave side with the concavity centrifugal to the ant body and, by having a curving radius of ca. 3 600–4 200 Å, they are able to diffract all the visible light spectrum giving the ant a metallic silvery or golden coloration.

At least *C. auricomus* (a black species densely covered by canaliculate hairs and assuming intense golden reflexes under strong illumination), when disturbed, produces a powerful, persistent odour of decaying citrus.

We suggest that the explanation for both types of coloration, i. e. dark-spotted with lighter maculae and metallic reflexes (the two are relatively rare in ants), should be a warning signal for predators (aposematism). The theory of aposematism dates back to CHARLES DARWIN (to whom it had been suggested by WALLACE) and there are numerous examples of animals with aposematic coloration in the literature. As already noted by GUILFORD (1990), most descriptions of the phenomenon stress the

simultaneous possession of conspicuous coloration and unpalatability among potential prey animals. However, FISHER (1930) noticed that there would be no selection pressure for the evolution of distastefulness unless the distasteful prey live in family groups. HARVEY (1983) extrapolates that the same explanation can apply to the evolution of aposematic coloration and several authors believe that kin selection can be invoked to explain aposematism (see review by GUILFORD, 1990). If this is true, social insects should be an ideal material for studying the evolution of unpalatability and, in fact, virtually all of them either sting or produce chemical repellents or both. Wasps, intuitively, may represent an ideal example, but there are few explicit mentions or descriptions of aposematic social insects in the literature (see e. g. the reviews by DELIGNE et al., 1981 and by HERMANN & BLUM, 1981). Hence, *Cephalotes* alone represents the most diverse example reported so far for a genus of probably aposematic social insects.

From Tab. 6 we show that 117 species of *Cephalotes*, out of 129 for which the worker caste is known (90.7%), present some kind of "unusual" coloration pattern. This proportion of remarkably coloured species falls to 84.4% among the soldiers and to 80.2% for the gynes.

From these data one could argue that the frequency of heterochromatic body parts in the three castes of *Cephalotes* parallels the rank in which these castes are encountered outside the nest.

If this is true, the short but highly risky period in which gynes are exposed to predation during the nuptial flight and colony foundation would be irrelevant in this context.

As it stands, this explanation is obviously too simplistic since one of the most remarkable coloration among ants in absolute terms is to be found in the gynes of *C. clypeatus*: yellow with 2 pairs of "eyes" on the gaster (Fig. 382). The workers and soldiers of the same species are equally yellow but they lack the "eyes". EMERY (1896) reports that callow *C. minutus* soldiers, normally with a completely black gaster, have four reddish spots on it – like gynes; these spots are destined to disappear when the pigmentation completes. This observation would also emphasise the importance of distinctive coloration for gynes.

It is not yet known with certainty if the chromatic signals of some species are correlated with the production of 4-heptanone and 4-heptanol as isolated from *C. varians* (a brown species to which it is difficult to attribute a powerful aposematic coloration), or with the presence of other (stronger) repellents or poisons.

GC-MS analyses of a sample of different castes of 8 *Cephalotes* species (not reported in this paper) reveal the presence of a wide array of compounds previously unreported in ants. The most astonishing record is probably the presence – in some species only – of camphor. Other compounds have been precisely identified but, if the repellent action of camphor on vertebrates and invertebrates is not in doubt, the difficulty with this approach is to assess the effect of small doses of some unnoticed compounds on the palatability of ants for a frog, a bird or a lizard.

On the other hand, many of the colorations listed in the table consist of relatively small variations and differences in intensity of the basic body colour.

Very often, the body parts differently coloured are very small, like the frontal carinae or the tip of the mesosomal spines. The adaptive significance of these less apparent colour patterns is likely to be mimetic since the main effect they have on a vertebrate eye is to "break up" the body contour of the ant (Fig. 383). Among castes

Fig. 381. *Cephalotes auricomus* (WHEELER). Gyne. Different morphologies of canaliculate hairs (with and without denticulate apex). These hairs diffract the light and give a golden or silvery metallic colour to the ant under strong illumination. It is assumed that the metallic coloration should be an aposematic signal since it is associated with the production of repellent pheromones.

Fig. 382. *Cephalotes clypeatus* (FABRICIUS). Gyne showing the two pairs of „eyes" on the gaster. This is probably the most manifest case of aposematic coloration in ants.

the differently coloured parts are respectively on the head in 96% of the workers, 75 % of the soldiers and 70% of the gynes, on the mesosoma in 38% of the workers, 41 % of the soldiers and 26% of the gynes, and on the gaster of 62% of the workers, 45% of the soldiers and 63% of the gynes of the species. The fact that the two extremes of the body are much more affected by heterochromatism than the center is also consistent with the mimetic explanation.

No *Cephalotes* species seem to use the sting for defence, but most of them bite their enemies. Their strong, heavily armoured integument can explain one of their behaviours already known from the literature for *C. atratus* (FOREL, 1912), namely entering wasp nests to prey on larvae.

Since the observation of WHEELER (1905: 104) that the nests of *C. varians* on the island of Andros have entrances of the same shape and size as the head of the soldiers, it has been assumed that the function of soldiers is one of blocking the nest

Fig. 383. *Cephalotes borgmeieri* (KEMPF). Worker on a branch of *Caesalpinia* where it had its nest in Lins (S. Paulo). The mimetism resulting from the similarity in colour between the bark and the ant is further improved by the ant's lighter body parts, like the frontal carinae. These interrupt the contour of the head making it less recognisable.

entrance (phragmosis). The term phragmosis was proposed much later by WHEELER (1926) for all the species of animals showing any kind of morphological adaptation serving the purpose of occluding the nest entrance. Cephalic phragmosis in ants has been observed only in some species of *Camponotus* (subfam. Formicinae) and *Cephalotes* (subfam. Myrmicinae), but morphological evidence suggests that this adaptation should be present also in some species of *Crematogaster* and *Pheidole* (both subfam. Myrmicinae) (WHEELER, 1926). As already stressed by WHEELER (l. c.) there is no doubt that phragmosis arose several times convergently among different groups of animals and among ants themselves.

The first direct observation of phragmotic behaviour in *Cephalotes* is from SANTSCHI (1919) who reports several *C. atratus* soldiers cooperating (successfully)

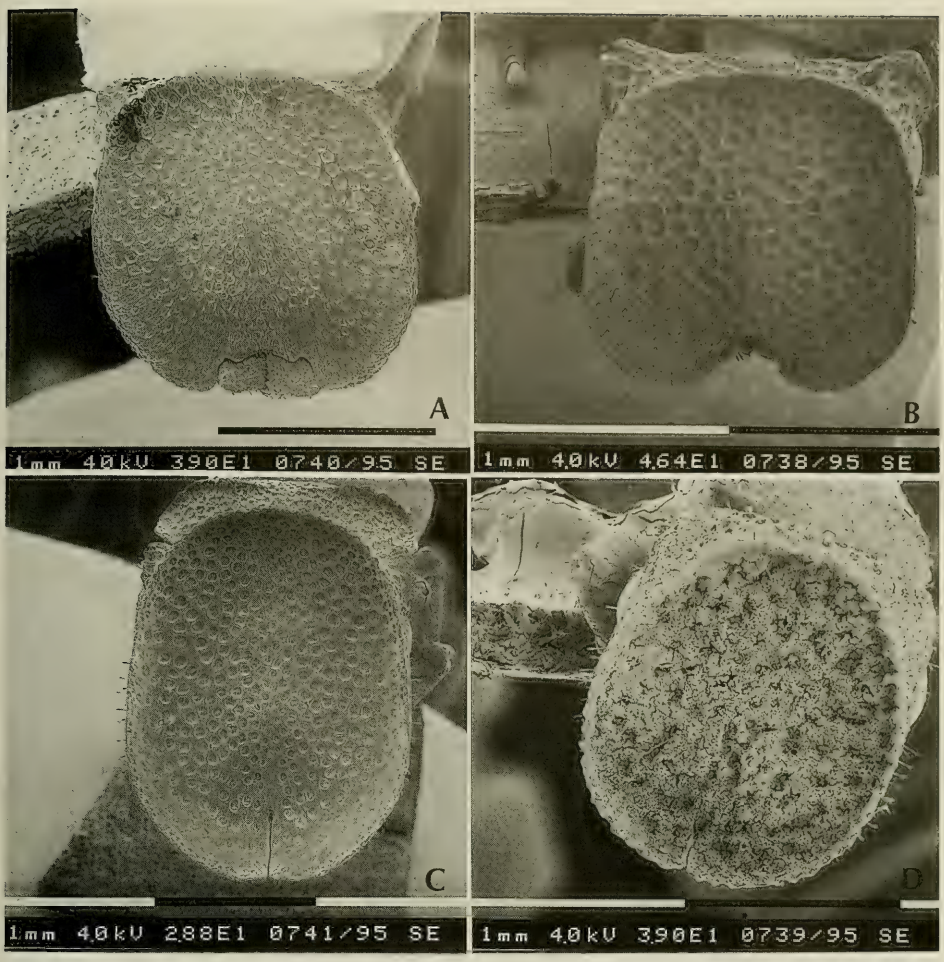

Fig. 384. Some examples of increasing adaptation to the phragmotic defence function among *Cephalotes* soldiers of different species. A: *C. texanus* (SANTSCHI), the head disc is nearly complete but the mandibles are free in dorsal view. B: *C. maculatus* (SMITH) with anteriorly expanded frontal carinae; the anterior border of the disc is deeply incised and the mandibles are partially visible. C: *C. varians* (SMITH), the frontal carinae touch each other medially completing the head disc; in dorsal view no cephalic appendages are visible. D: *C. setulifer* (EMERY), the head disc is complete and rendered mimetic by a layer of encrustation of probable glandular origin.

to close a large nest entrance during an attack by an *Eciton* colony in Venezuela. Confirmation of this behaviour came only in 1952 from KEMPF for *C. pinelii*, and its first (and only) detailed description for *C. texanus* (which has been shown to use the head and the pronotum for this function) by CREIGHTON & GREGG followed in 1954. One of us (MLDA) observed phragmosis exercised by workers of *C. auricomus* in the Dominican Republic, a species without differentiated soldiers. DELABIE (1994) gives abundant evidence that in *C. pusillus* – a species with workers and soldiers – workers may also exercise the phragmotic function. This information allows us to trace among existing species the presence of a logically necessary step

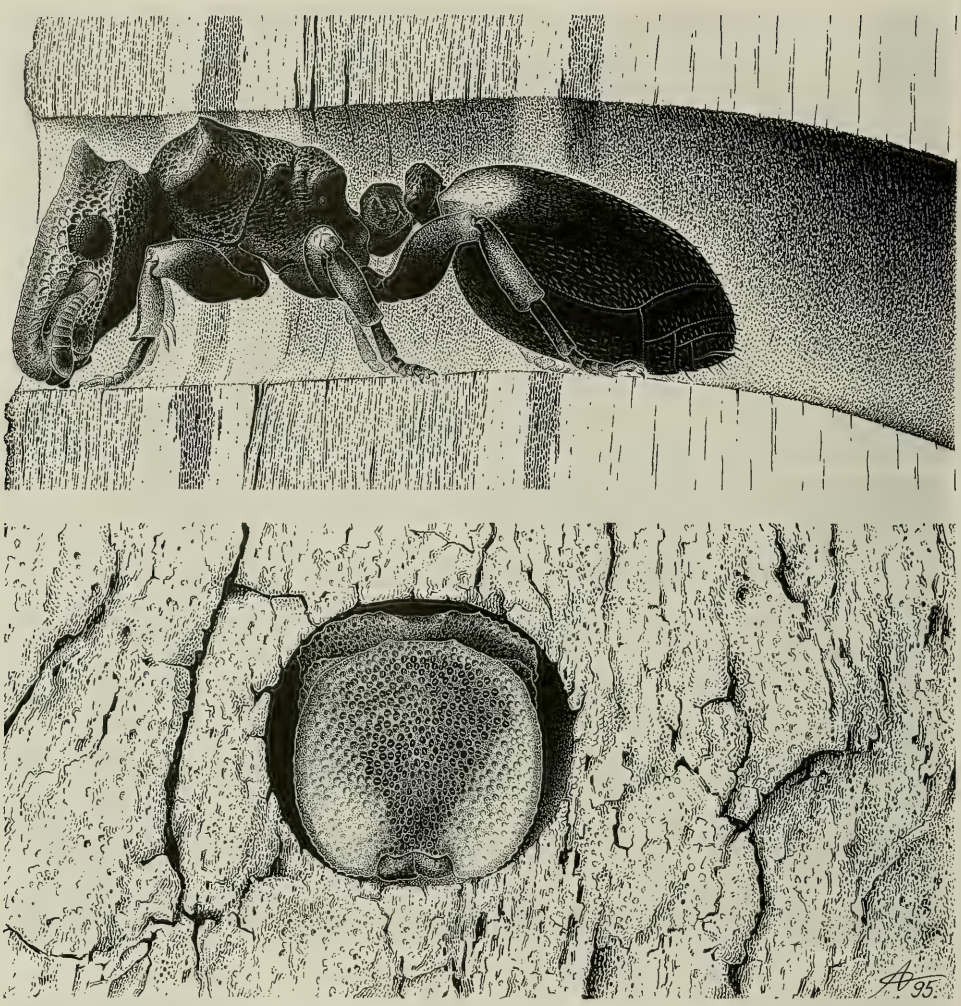

Fig. 385. *Cephalotes texanus* (SANTSCHI). A soldier closes the entrance of a nest derived from tunnels dug by beetle larvae in dead wood. To better fit its body size to the size of the tunnel it blocks the upper part of the entrance with the pronotal carina while the head is adjusted to fit the remaining space. The pronotal carina is a structure characteristic of the *Cephalotes* soldiers. In several species both the cephalic disc and the pronotal carina of soldiers are "transmitted" to different extents to gynes where they have no functional significance.

for the evolution of phragmosis. In other words, the most probable origin of morphologically specialised phragmotic soldiers in *Cephalotes* is to be found among selection pressures favouring improvement of a pre-existing technique of defence of the nest entrance and not in a secondary specialisation of already available large-headed individuals to block the entrance with their head.

Among *Cephalotes* soldiers, some species show a remarkable morphological adaptation to phragmosis. First the vertexal area flattens into a semicircular shape and then the frontal carinae expand first anterolaterally and then join each other

Fig. 386. *Cephalotes betoi* DE ANDRADE. Top: soldier, hair-like cuticular projections (sensilla auricillica) on the upper head surface. Bottom: worker, same cuticular projections as in the soldier but not associated with a true foveal socket.

medially until the cephalic disc is complete. Different steps of this morphoclinal trend are still recognisable among different species (Fig. 384).

Another important fact in the *Cephalotes* caste system can be explained by means of the observations of CREIGHTON & GREGG (1954). Virtually all soldiers of this genus, with or without a head disc, can be easily distinguished from workers by the presence of a unique morphological feature: a transverse pronotal carina. The carina is an integral part of the morphological adaptation to phragmosis since it serves the purpose of blocking the nest entrance together with the head (Fig. 385). Existence of such a typical and functionally clear trait stresses the importance of the nest defence selection pressures that governed the origin of the soldier caste in the genus.

The logical explanation for the origin of the pronotal carina is to be found in the habit of these ants of nesting in pre-existing wood cavities. The addition to the head with respect to its entrance blocking function of a second, movable, body part (i. e. the pronotum) allows the ants to adjust themselves to pre-existing plant cavities of different size.

WILSON (1976 b) adds that, in *C. varians*, the shield-shaped head is used also to "bulldoze" intruders out of the nest, though this same function is also performed by workers without shield.

The cephalic capsule of most *Cephalotes* species bears, dorsally, numerous, deep piligerous pits; at least in some species the borders of these pits are equipped with a sensillum auricillicum (Fig. 386, top) supposed to allow discrimination of nestmates from intruders (BUREN et al., 1977; HERMANN & BLUM, 1981). Morphologically very similar cuticular projections, however, may exist independently of the presence of a piligerous pit (Fig. 386, bottom). In some species (e. g. *wheeleri*, Figs. 267, 268, *insularis*, Figs. 271, 272, *guayaki*, Figs. 311, 312, etc.), the sensilla auricillica are present only in soldiers and gynes and not, or in very reduced numbers, in workers and never in males. It seems that the enormous variety of hair morphologies present in *Cephalotes* is the joint product of two main trends still recognisable at various degrees among different species. These trends are (1) a tendency to flatten and broaden originally thin and pointed hairs (Fig. 387) and the formation of deeper integumental pits hosting each hair (Fig. 388). The so-called sensilla auricillica are a good example in which hair flattening and pit deepening are shared. The extreme end of this hypothetical morphocline seems to be represented by *C. foliaceus* whose hairs are hosted in deep pits and assume the shape of palm leaves (Fig. 389). This morphology defies explanation.

Soldiers of different species are often collected with the cephalic disc encrusted by extraneous material. WHEELER (1942) suggested that this could have a mimetic function, i. e. it may serve to reduce the chances of visual discovery by its enemies of an individual blocking the nest entrance. WHEELER & HÖLLDOBLER (1985) accepted WHEELER's hypothesis and offered SEM circumstantial evidence that the covering materials could be produced by glands of the ant itself.

One might think that there is some contradiction between the presence of specialised sensilla over the head and the covering of the same part of the body by extraneous material but the observations reported above refer to different species and the SEM micrographs produced by WHEELER & HÖLLDOBLER (l. c.) show no sensilla auricillica but a good number of sensory hairs free from camouflage material.

We also observed similar encrustations over the head of the soldiers and gynes of most species of the *pallens* clade (Fig. 390) but other species of other clades (e. g. *coffeae*, *setulifer*) may also have them. The presence or absence and the thickness of the

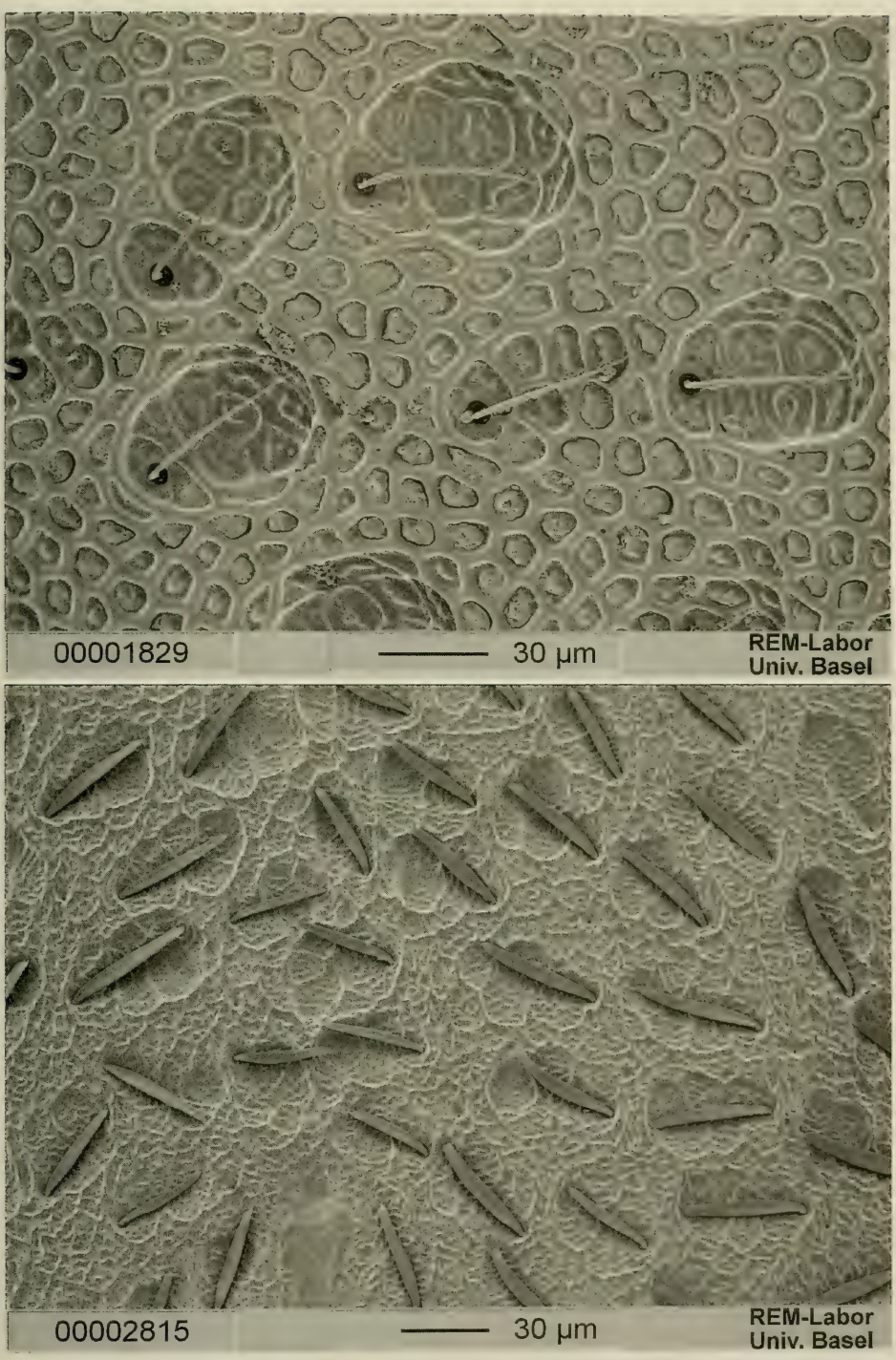

Fig. 387. Cephalic hairs of workers of *C. oculatus* (SPINOLA) (top) and *simillimus* (KEMPF) (bottom) suggesting the tendency to broaden originally long and pointed hairs.

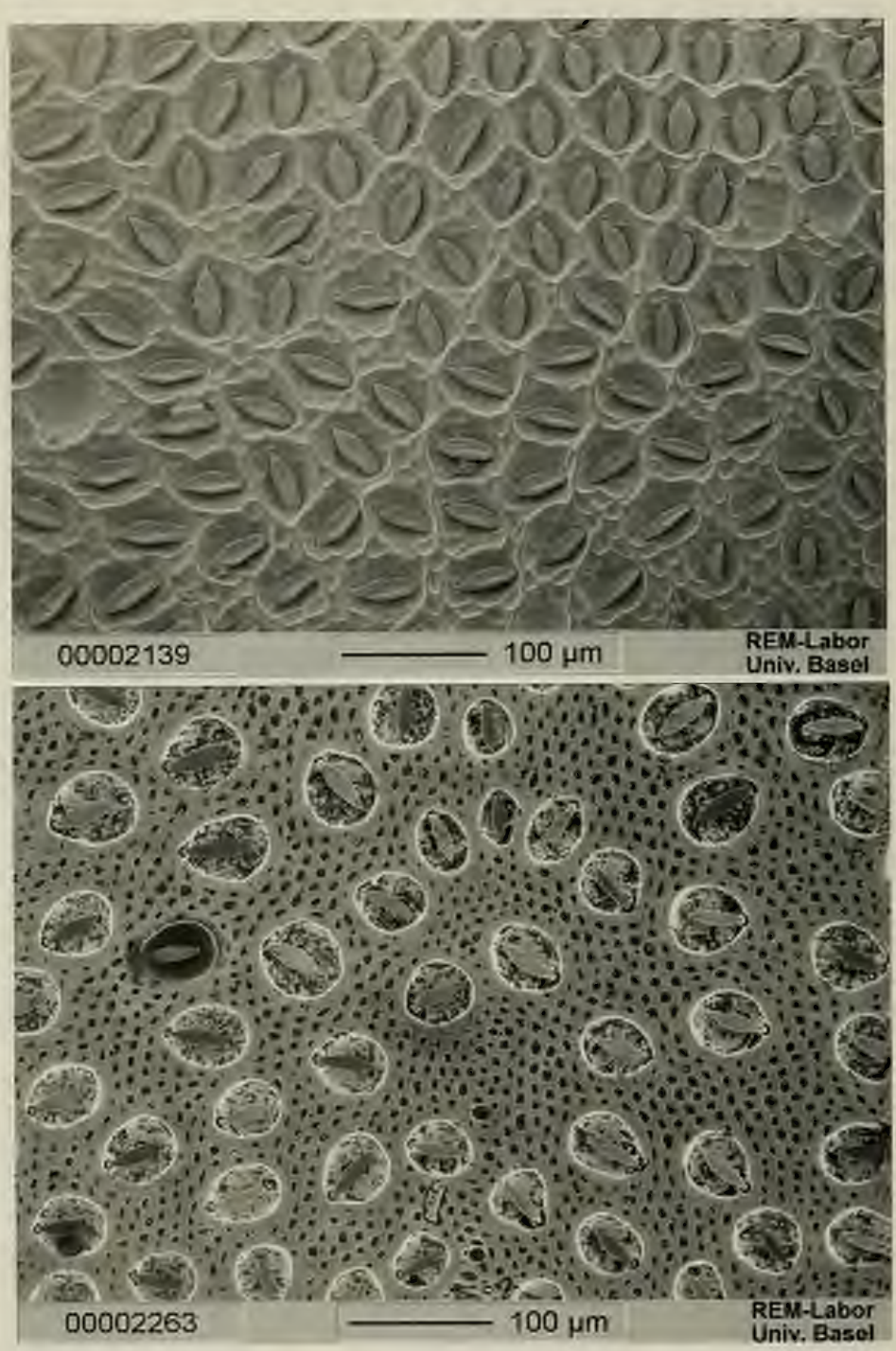

Fig. 388. Cephalic hairs of *C. mompox* (De Andrade) workers (top) and *depressus* (Klug) soldiers (bottom) showing flat hairs accommodated into integumental pits of different depth.

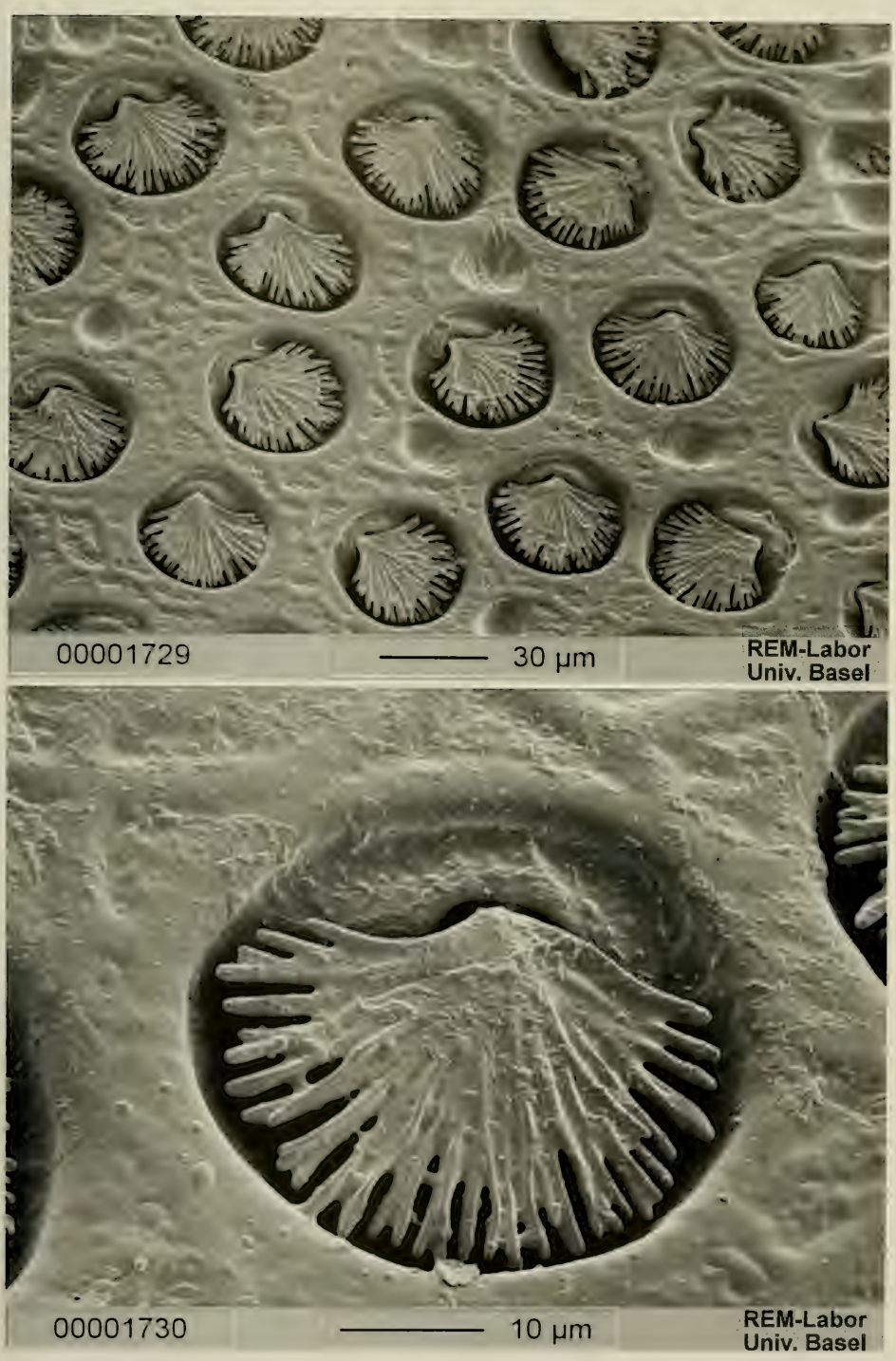

Fig. 389. Palm-leaf-shaped hairs on the mesosoma of *C. foliacens* (EMERY) (top) and details of a single hair (bottom). The function of these hairs remains unknown.

encrustations is individually variable within each species. Clean individuals may show a high density of integumental pores (Fig. 391). We concur with WHEELER & HÖLLDOBLER (1985) in their interpretation that these pores are probably glandular openings intended to extrude the encrusting material.

All *Cephalotes* species share a thick, hard integument bearing spines and crests on different body parts. These, of course, have a primary function in defence and defence appears to be the strongest selection pressure with which these ants have been confronted. CORN (1976) describes how, while holding specimens of *C. atratus* and *C. placidus* in the hand, "the two pairs of thoracic spines, which are very sturdy, were enough to make this observer momentarily think that she was being stung while handling them". It is likely that the same sensation can be extended to any vertebrate predator attempting to bite these ants. HUNT (1983), from morphological inspection of *C. atratus*, suggests a strategy of resistance to predation as opposed to predator avoidance as it is the case for most Myrmicinae. Other species of *Cephalotes* appear to have developed different mechanisms of predation avoidance, the most remarkable of which is probably their capacity to run backwards as rapidly as forwards (WEBER, 1934; EIDMANN, 1936), a rare trait among ants.

Several *Cephalotes* species, when attacked or disturbed, simply fold the antennae in the antennal scrobes, flex the legs close to the mesosoma and gaster (often equipped with dorsal expansions and lamellae which can cover the appendages entirely) and profit from their hard, armoured integument to protect themselves, much like small turtles could do. This passive defence mechanism is particularly easy to observe while holding a specimen with a forceps but *Cephalotes* workers flatten themselves in a similar manner against branch surfaces if confronted with workers of other ant genera like *Camponotus* and *Azteca* (COYLE, 1966; ADAMS, 1990). The diversity of species-specific passive defence solutions in *Cephalotes* is greater than its own taxonomic diversity since presence, size and distribution of body spines and lamellae vary not only according to the species but also to the caste.

The female castes of all *Cephalotes* species bear some kind of lamellae or expansions on one or more body parts. In fact, one of the salient characters of the genus are the broad frontal carinae which serve to cover the antennae. This contrasts with the male morphology where neither lamellae nor remarkable spines are present. In the sister genus *Procryptocerus* the frontal carinae are reduced (compared with those of *Cephalotes*) but expanded frontal carinae are the rule in *Cataulacus* where they are shared by males as well.

A minority of *Cephalotes* species have cephalic expansions other than the frontal carinae. Additional expansions are present in 27% of the workers, 31% of the gynes and 43% of the soldiers. The gyne and soldier figures, however, are misleading since several species possess "only" a cephalic disc which may be considered as a single pair of very expanded frontal carinae. The additional cephalic expansions invariably correspond to a broadening of the vertexal angles which can facilitate the phragmotic function and, to a lesser extent, protect part of the forelegs. Protection of the legs, of course, is served essentially by expansions of the mesosoma, of the pedicel, and, in part, of the gaster. Mesosomal expansions are present to different extents in 79% of the workers, 98% of the soldiers and 30% of the gynes. The only two species having a soldier caste without mesosomal lamellar expansions of any kind are *alfaroi* and *opacus*. These figures are not too dissimilar from those of the expansions of the pedicel and gaster which are present in 91% of the workers, 93% of the soldiers and 80% of the gynes.

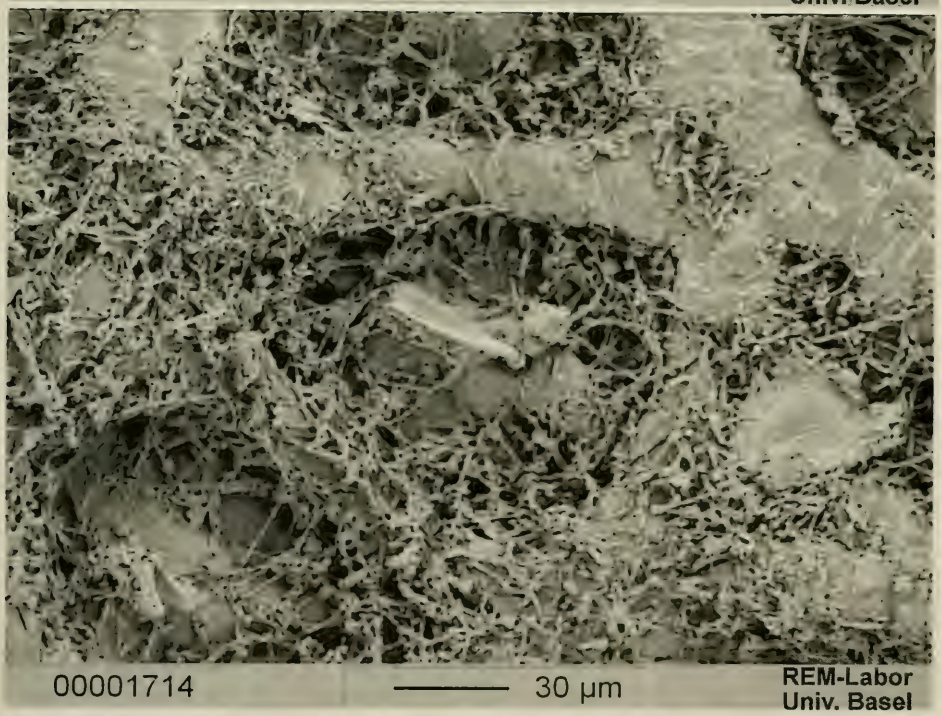

Fig. 390. *Cephalotes pallidus* DE ANDRADE, soldier. Details of the cephalic disc showing the encrustation of filiform material supposed to have the function of rendering the cephalic disc less obvious to predators.

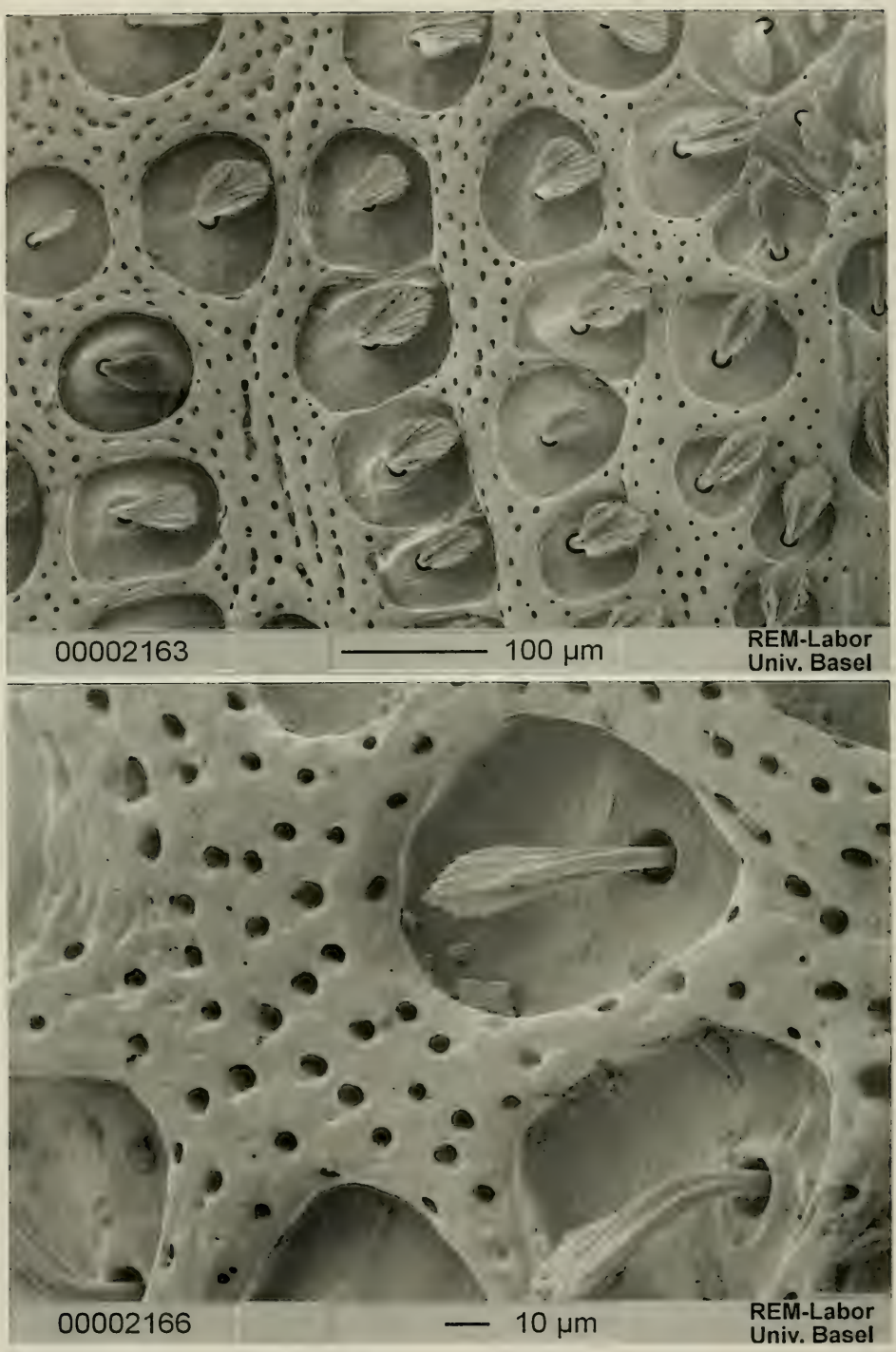

Fig. 391. *Cephalotes porrasi* (WHEELER), gyne. Details of the cephalic disc of a clean individual showing the numerous pores. It is speculated that the pores are glandular openings through which the mimetic filaments are extruded to the surface.

Tab. 7.1. Different morphological adaptations to passive defence in *Cephalotes* female castes. Teeth and spines are interpreted as a defence against vertebrate predation. Expansions of different body parts serve to protect the appendages and should function primarily against other ants and arthropods in general. Species *adolphi* to *crenaticeps*. Abbreviations: l. = large; s. = small, sp. = spines, exp. = expansions.

	Worker			Soldier			Gyne		
	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster
adolphi	4 l. exp.	12-14 teeth	4 teeth+2 s. exp.	?	?	?	?	?	?
alfaroi	4 l. sp.+2 l. exp.	4 s. teeth+6 l. sp.	teeth+2 s. exp.	2-4 s. sp.+2 l. exp.	6 l.+ 2 s. sp.	4 teeth+2 s. exp.	4 s. teeth+2 l. exp.	2 s. teeth+ 2 l. sp.	4 s. teeth+2 s. exp.
angustus	0-2 s.+2 l. exp.	14-18 s. teeth+2 s.exp.	4 teeth+ 2 s. exp.	disc	4 s. teeth+2 sp.+4 s. exp.	4 teeth+2 s. exp.	disc	6 teeth	4 teeth+2 s. exp.
argentiventris	2 l. exp.	2-4 teeth+2 s. +2 l. sp.	2 teeth+2 s. sp.+2 s. exp.	—	—	—	?	?	?
atratus	0-2 teeth+4 l. sp.+2 l. exp.	0-2 teeth+4 l. sp.	0-4 s. teeth+2 s. exp.	—	—	—	2-6 s. teeth+2 l. exp.	4 sp.	2 s. exp.
auriger	2 l. exp.	6 teeth+2 s. exp.	2 teeth+2 s. sp.+2 s. exp.	?	?	?	?	?	?
auricomus	2 l. exp.	2-4 teeth+2 s. +2 l. sp.	2 teeth+2 s. sp.+2 s. exp.	—	—	—	2 l. exp.	4 s. sp.	2 s. exp.
basalis	2 teeth+2 l. exp.	2 teeth+4 s. +2 l. sp.	4 l. sp.+2 s. exp.	2 teeth+2 l. exp.	6 teeth+2 s. sp.+4 l. exp.	4 sp.+2 s. exp.	2 teeth+2 l. exp.	4 teeth+2 s. sp.	4 sp.+ 2 s. exp.
betoi	4 teeth+2 l. exp.	6 teeth+2 l. exp.	4 sp.+2 s. exp.	part. disc+4-6 teeth	2 teeth+4 s.+2 l. exp.	4 sp.+2 s. exp.	4 s. teeth+2 l. exp.	4 teeth	4 s. teeth+s. exp.
biguttatus	2 s. teeth+2 s. exp.	2 s. teeth+2 s.+2 l. exp.	2 teeth+2 sp.+2 s. exp.	2 teeth+2 l. exp.	2 teeth+4 l. exp.	2 teeth+2 s. exp.	2-4 s. teeth+2 l. exp.	2 s. teeth	2 teeth+2 s. exp.
bimaculatus	2 l. exp.	4 s. teeth+2 s. exp.	2 s.+2 l. teeth	disc	4 s. exp.	4 s. teeth+2 s. exp.	disc	4 s. exp.	4 s. teeth+2 s. exp.
bivestitus	2 l. exp.	10-12 s. teeth +2 s. exp.	4 s. teeth+2 exp.	disc	4 teeth+4 exp.	4 teeth+2 exp.	disc	4 s. teeth	4 s. teeth+2 exp.
bohlsi	0-2 s. teeth+2+2 l. exp.	14 s. teeth+2 s. exp.	4 teeth+2 exp.	disc	2 s.+2 l. teeth+2 exp.	4 teeth+2 exp.	?	?	?
borgmeieri	4 s. teeth+2 l. exp.	4 teeth+2 sp. +2 l. exp.	4 sp.+2 exp.	part. disc+4-6 s. teeth	2 teeth+4 s.+2 l. exp.	4 sp.+2 s. exp.	4-6 s. teeth +2 exp.	6 s. teeth	2 teeth+2 s. exp.
bruchi	0-2 s.+2 l. exp.	6-8 s. teeth+2 exp.	4 teeth+2 exp.	part. disc+2 s. exp.	2 teeth+4 s. exp.	4 teeth+2 exp.	part. disc+2 s. exp.	2 s.+2 l. teeth	2 teeth+2 exp.
chacmul	2 l. exp.	14-18 s. teeth +2 s. exp.	4 sp.+2 exp.	disc+2 exp.	4 s. teeth+4 exp.	4 sp.+s. exp.	?	?	?
christopherseni	4 l. exp.	8 s. teeth+6 sp.+2 s. exp.	4 teeth+2 exp.	2 teeth +2+2 l. exp.	6 s.+4 l. teeth+2 sp.+4 s. exp.	4 teeth+2 exp.	2 s. teeth+2 l. exp.	4 teeth	2 s. teeth+2 exp.
clypeatus	2 sp.+2 l. exp.	2 s+4 l. sp.+4 l. exp.	4 sp.+2 l. exp.	4 sp.+2 l. exp.	2 s+4 l. sp.+4 l. exp.	4 sp.+2 l. exp.	4 teeth+2 l. exp.	2 s. sp.+2 s. exp.	0-2 s. teeth+2 exp.
coffeae	2 l. exp.	14 s. teeth+2 s. exp.	4 teeth+2 s. exp.	disc	6 s. teeth+2 exp.	4 teeth+2 s. exp.	disc	2-6 s. teeth	2 s.+2 l. teeth+2 s. exp.
columbicus	2 s.+2 l. exp.	6 s. teeth+2 s.+2 l. sp.	2-4 teeth+2 exp.	2 l. exp.	6 s.+2 l. teeth+2 l. sp.+ exp.	2 teeth+2 s. exp.	2 l. exp.	4 teeth	0-2 s. teeth+2 s. exp.
complanatus	2 s. teeth+2 l. exp.	4 l. teeth+2 s. sp.+2 l. exp.	4 sp.+2 exp.	2 s. teeth+2 l. exp.	2 teeth+6 l. exp.	4 sp.+2 exp.	2 s. teeth+2 l. exp.	2 teeth+2 sp.	2 teeth+2 sp.+2 s. exp.
conspersus	0-2 s.+2 l. exp.	18-20 s. teeth +2 s. exp.	4 teeth+2 exp.	disc+2 exp.	2 teeth+2 sp.+4 exp.	4 teeth+2 exp.	?	?	?
cordatus	4-6 s. teeth+0-2 s.+2 l. exp.	4 teeth+2 sp. +2 l. exp.	4 sp.+2 exp.	disc+2 teeth	4 s.+2 l. exp.	4 sp.+2 exp.	part. disc+2 s. teeth	4 s. teeth	2 s. teeth+4 exp.
cordiae	2 l. exp.	2 teeth+2 l. sp.+2 exp.	4 sp.+2 s. exp.	2 l. exp.	2 teeth+2 l. sp.+2 exp.	4 sp.+2 s. exp.	2 l. exp.	4 teeth	4 teeth
cordiventris	2 teeth+2 l. exp.	4 l. teeth+2 sp.+2 l. exp.	4 sp.+2 exp.	4 s. teeth+2 l. exp.	6 teeth+2 l. exp.	4 sp.+2 s. exp.	2 s. teeth+2 l. exp.	2 s.+2 l. teeth	4 s. teeth
crenaticeps	2 l. exp.	0-2 s. teeth+2 exp.	2 s.+2 l. teeth	disc+2 s. teeth+2 exp.	6 s. teeth+2 exp.	2 s.+2 l. teeth	disc+2 s. teeth+2 exp.	6 s. teeth	2 s.+2 l. teeth

Tab. 7.2. Different morphological adaptations to passive defence in *Cephalotes* female castes. Teeth and spines are interpreted as a defence against vertebrate predation. Expansions of different body parts serve to protect the appendages and should function primarily against other ants and arthropods in general. Species *cristatus* to *insularis*. Abbreviations: l. = large; s. = small, sp. = spines, exp. = expansions.

	Worker			Soldier			Gyne		
	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster
cristatus	2 s.+4 teeth+2 l. exp.	6 l. teeth+2 sp.+2 l. exp.	4 sp.+2 exp.	disc+6 teeth	4 teeth+2+2 l. exp.	4 sp.+2 exp.	part. disc+4-6 s. teeth	4 s. teeth+2 sp.	2 sp.+2 exp.
curvistriatus	2 l. exp.	14 s. teeth+2 s. exp.	2 l. teeth+2 sp.+2 s. exp.	disc	4-6 s. teeth+4 exp.	4 l. teeth	disc	2 teeth	2 s.+2 l. teeth
decolor	2 l. exp.	2 teeth+4 l. exp.	4 sp.+2 l. exp.	disc+2 l. exp.	2-4 teeth+4 exp.	4 l. teeth+2 l. exp.	disc+2 exp.	2-4 teeth	2-4 teeth+2 l. exp.
decoloratus	2 l. exp.	2 teeth+4 l. exp.	4 sp.+2 exp.	disc+2 s. teeth	2-4 teeth+4 exp.	4 l. teeth+2 exp.	disc+2 exp.	2-4 teeth	2-4 teeth+2 exp.
dentidorsum	4 l. exp.	12-14 teeth	4 teeth+2 s. exp.	?	?	?	?	?	?
depressus	4 s. teeth+2 l. exp.	6 teeth+2 sp. +2 l. exp.	2 l. teeth+2 sp.+2 s. exp.	part. disc	0-2 teeth+2 s.+2 l. exp.	4 teeth	2 l. exp.	4 s. teeth	4 s. teeth
duckei	2 s.+2 l. exp.	4 teeth+2 sp. +4 l. exp.	4 teeth+2 l. exp.	part. disc+2 s. teeth	4 s. teeth+2 sp.+2 s.+4 l. exp.	4 teeth+2 l. exp.	part. disc+2 teeth	4-6 teeth	0-2 s. teeth+2 l. exp.
ecuadorialis	2 s.+2 l. exp.	2 s. teeth +2 exp.	2 s.+2 l. teeth+2 s. exp.	?	?	?	disc	4 s. teeth	2 s. teeth
eduarduli	2 s.+2 l. teeth+2 l. exp.	6 teeth+2 sp. +2 l. exp.	4 sp.	part. disc+4-6 s. teeth	2 s.+4 l. exp.	4 sp.	2-4 s. teeth+2 l. exp.	4-6 s. teeth	0-2 s.+2 teeth
emeryi	2 l. exp.	2 s. teeth+2 l. exp.	2 s.+2 teeth	?	?	?	?	?	?
femoralis	2 teeth+2 l. exp.	2-4 s. teeth +4 sp.	4 l. sp.+2 exp.	?	?	?	?	?	?
fiebrigi	0-2 s. teeth+2 l. exp.	12-14 s. teeth	4 sp.+2 exp.	disc	6 s. teeth+2 exp.	4 sp.+2 exp.	disc	4 teeth	4 teeth+2 exp.
flavigaster	2 l. exp.	2+2 l. sp.	2 teeth+2 sp.+2 s. exp.	—	—	—	?	?	?
foliaceus	4 l. exp.	6 l. exp.	2 l. sp.+4 l. exp.	disc+2 l. exp.	2 s. teeth+6. exp.	2 sp.+4 l. exp.	?	?	?
fossithorax	2 l. exp.	10-14 s. teeth +2 s. exp.	2 s. teeth +4 l. exp.	disc	2 teeth+4 exp.	2 teeth+4 l. exp.	disc	2 teeth+2 exp.	0-2 s. teeth+4 exp.
frigidus	0-2 s.+2 l. exp.	14-16 s. teeth +2 s. exp.	4 s. sp. +2 s. exp.	disc+2 exp.	2 s. + 2 l. teeth+4 exp.	2 teeth+2 exp.	disc+2 exp.	2 s.+2 l. teeth	2 s. teeth+4 exp.
goeldii	4 l. exp.	18-20 s. teeth +2 exp.	4 teeth +2 exp.	disc+2 l. exp.	2-4 s.+2l. teeth+4l. exp.	2 teeth+4 l. exp.	disc+2 l. exp.	2s.+2.teeth +2 exp.	2s. teeth+4 exp.
goniodontus	2 s. teeth+2 s.+2 l. exp.	2 s. teeth +4 l. exp.	4 sp.+2 s. exp.	part. disc+2 teeth+2 s. exp.	0-2 s. teeth+4 l. exp.	4 teeth +2 s. exp.	?	?	?
grandinosus	2 s.+2 l. exp.	2-4 s. teeth +4 l. exp.	6 exp.	disc+2 exp.	4-6 s. teeth+2 s. exp.	6 exp.	disc+2 exp.	4 teeth	2 s.+2 l. exp.
guayaki	2 l. exp.	12-14 s. teeth +2 s. exp.	4 sp.+2 exp.	disc+s. exp.	2 s.+2 l. teeth+2 exp.	4 teeth+2 s. exp.	disc+2 exp.	2-4 s. teeth	4 teeth+2 exp.
hamulus	2 l. exp.	0-2 s. teeth+2 s.+2 l. sp.	2 teeth+2 sp.+2 s. exp.	—	—	—	2 l. exp.	4 teeth	?
hirsutus	2 l. exp.	4-6 s. teeth+2 s. sp.+2 s. exp.	4 sp.	?	?	?	?	?	?
inaequalis	4 l. exp.	6 teeth+4 s. sp. +2 exp.	4 teeth+2 l. exp.	2 s. teeth+2 s.+2 l. exp.	4 teeth+2 sp.+4 exp.	4 teeth+2 l. exp.	2+2 l. exp.	2 teeth	4 teeth+2 exp.
inca	2 s. teeth+2 l. exp.	2 s.+4 l. teeth+ 2 l. sp.+2 l. exp.	2+2 l. sp.+2 exp.	?	?	?	2 s. teeth+2 l. exp.	6 teeth	4 sp.+2 s. exp.
incertus	2 l. exp.	6 s. exp.	6 s. exp.	disc+2 exp.	6 s. exp.	6 s. exp.	disc+2 exp.	2 s. teeth+2 s. exp.	4-6 s. exp.
insularis	2 l. exp.	6-8 s. teeth+2 sp.+2 s. exp.	4 sp.	disc+2 exp.	4 teeth+2 exp.	2 s.+2 sp.	disc+2 exp.	2 teeth	0

Tab. 7.3. Different morphological adaptations to passive defence in *Cephalotes* female castes. Teeth and spines are interpreted as a defence against vertebrate predation. Expansions of different body parts serve to protect the appendages and should function primarily against other ants and arthropods in general. Species *jamaicensis* to *palta*. Abbreviations: l. = large; s. = small, sp. = spines, exp. = expansions.

	Worker			Soldier			Gyne		
	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster
jamaicensis	2 l. exp.	6 s. exp.	4 s. sp.+2 exp.	disc+2 exp.	2 s.+2 l. teeth+4 exp.	4 teeth+2 l. exp.	?	?	?
jheringi	2 l. exp.	14-16 s. teeth +2 s. exp.	4 teeth+2 l. exp.	disc	2 s.+2 l. teeth+4 exp.	4 teeth+2 l. exp.	disc	2 teeth	4 s. teeth+2 exp.
klugi	?	?	?	?	?	?	disc+2 exp.	2 teeth+2 exp.	4 exp.
kukulcan	2 l. exp.	2 teeth+4 s. exp.	4 spine+2 exp.	disc+2 exp.	6 s. exp.	2 teeth+4 exp.	disc+2 s. exp.	4 teeth	0-2 s. teeth+4 exp.
laminatus	4 l. exp.	4 s.+6 l. teeth +4 sp.	4 l. teeth+2 l. exp.	2 s. teeth+2+2 l. exp.	4 s. teeth+2 sp.+2 exp.	4 teeth+2 exp.	2 l. exp.	4 sp.	4 exp.
lanuginosus	2 l. exp.	4 s.+4 l. teeth +2 exp.	4 sp.+2 exp.	disc+2 exp.	2 s.+2 l. teeth+2 exp.	2 teeth+4 exp.	disc+2 s. exp.	4 s. teeth	0-2 s. teeth+4 exp.
lenca	2 l. exp.	14-18 s. teeth +2 s. exp.	2 s.+2 l. sp.+2 exp.	?	?	?	?	?	?
liepini	2 l. exp.	2 s. teeth+4 exp.	6 exp.	disc+2 exp.	6 exp.	6 exp.	?	?	?
liogaster	0-2 s. teeth+2 l. exp.	10-12 s. teeth +2 exp.	4 sp.+2 exp.	disc+2 s. exp.	2-4 s. teeth+4 exp.	2 teeth+4 exp.	disc+2 exp.	4 s. teeth	0-2 s. teeth+4 exp.
maculatus	2 l. exp.	2 s. teeth+4 exp.	6 exp.	disc+2 exp.	2-6 s. teeth+6 exp.	6 exp.	disc+2 s. exp.	4 s. teeth	0-2 s, teeth+4 exp.
manni	2 l. exp.	14 s. teeth +2 s.+2 l. exp.	4 sp.+2 exp.	2+2 l. exp.	6 exp.	4 s. sp.+2 l. exp.	?	?	?
marginatus	0-2 teeth+4 l. sp.+2 l. exp.	0-2 teeth+4 l . sp.	0-4 s. teeth+2 s. exp.	—	—	—	2-6 s. teeth+2 l. exp.	4 sp.	2 s. exp.
membranaceus	2 sp.+2 l. exp.	2 s+4 l. sp. +4 l. exp.	4 sp.+2 l. exp.	part. disc+4 sp.	2 s.+4 l. sp.+4 l. exp.	4 sp.+2 l. exp.	part. disc+4 s. teeth	2 s. sp.+2 s. exp.	2 teeth+2 exp.
minutus	2 s.+2 l. exp.	8 s. teeth+2 s. +2 l. sp.+2 exp	4 teeth+2 exp.	2 l. exp.	2 sp.+6 exp.	4 teeth+2 exp.	2 l. exp.	2 s.+2 l. teeth	0-2 s.+2 teeth+2 exp.
mompox	2 teeth+2 l. exp.	2 s. teeth+4 s. +2 l. sp.	4 sp.+2 exp.	?	?	?	?	?	?
multispinosus	2 s. teeth+2 s.+2 l. exp.	2 s. teeth+4 l. exp.	4 sp.+2 s. exp.	part. disc+2 teeth+2 s. exp.	2 teeth+4 exp.	2 teeth+2 sp.+2 exp.	part. disc+2 teeth+2 exp.	2 exp.	2 s. exp.
nilpiei	2 l. exp.	2 s. teeth+4 exp.	6 exp.	disc+2 exp.	2 s. teeth+6 exp.	6 exp.	?	?	?
notatus	2 l. exp.	20-22 s. teeth +2 s. exp.	4 teeth+2 exp.	disc+2 l. exp.	4-6 s. teeth+4 l. exp.	4 teeth+2 s. exp.	disc+2 l. exp.	2 s.+2 l. teeth+2 s. exp.	0-2 s. teeth+4 s. exp.
oculatus	4 teeth+4 s. sp.+2 l. exp.	2 teeth+4 l. sp.	2 exp.	—	—	—	4 s.+4 l. teeth+2 l. exp.	4 s. sp.	2 s. exp.
opacus	2-4 s. teeth+4 s. sp.+2 l. exp.	4 sp.	0-2 s. to l. exp.	6 teeth+2 s. sp.+2 l. exp.	4 s.+2 l. sp.	2 exp.	2-4 s.+4 l. teeth+2 l. exp.	4 sp.	2 s. exp.
pallens	2 l. exp.	4 s. teeth+4 exp.	4 sp.+2 l. exp.	disc+2 exp.	2 s. teeth+6 exp.	4 l. teeth+2 expansions	disc+2 s. exp.	2-4 s. teeth +2 s. exp.	2-4 s. teeth +2 l. exp.
pallidicephalus	0-2 s.+2 l. exp.	16-18 s. teeth +2 s. exp.	4 l. teeth+2 exp.	disc+2 exp.	2 s.+2 l. teeth+4 exp.	4 l. teeth+2 exp.	disc+0-2 s. exp.	2 s.+2 l. teeth	4 teeth+2 exp.
pallidoides	2 l. exp.	2 teeth+4 exp.	4 sp.+2 exp.	disc+2 s. exp.	0-4 s.+2 l. teeth+4 exp.	4 teeth+2 l. exp.	disc+2 exp.	2-4 s. teeth	2-4 s. teeth +2 l. exp.
pallidus	2 l. exp.	4 exp.	4 sp.+2 l. exp.	disc+2 s. exp.	2 teeth+4 exp.	4 teeth+2 exp.	disc+2 s. exp.	4 s. teeth	0-2 s.+2 l. teeth+2 l. exp.
palta	0-2 s.+2 l. exp.	16-18 s. teeth +2 exp.	4 teeth+2 exp.	disc+2 exp.	2 s.+2 l. teeth+4 exp.	2 s.+2 teeth+2 exp.	?	?	?

Tab. 7.4. Different morphological adaptations to passive defence in *Cephalotes* female castes. Teeth and spines are interpreted as a defence against vertebrate predation. Expansions of different body parts serve to protect the appendages and should function primarily against other ants and arthropods in general. Species *palustris* to *spinosus*. Abbreviations: l. = large; s. = small, sp. = spines, exp. = expansions.

	Worker			Soldier			Gyne		
	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster
palustris	2+2 l. exp.	6 teeth+2 sp. +2 l. exp.	4 sp.+2 exp.	disc+4 s. teeth	2 teeth+4 l. exp.	4 l. teeth	?	?	?
patei	2 teeth+2 l. exp.	4 s. teeth+2 l. exp.	4 s. teeth+2 s. exp.	disc+2 s. teeth+2 exp.	4 s. teeth+2 s.+2 l. exp.	4 s. teeth+2 s. exp.	disc+2 exp.	2 s. teeth+2 exp.	2 s. exp.
patellaris	2 l. exp.	6 exp.	4 sp.+2 l. exp.	disc+2 exp.	2 s. teeth+4 exp.	4 teeth+2 l. exp.	disc+2 exp.	2 s. teeth	0-2 s.+2 teeth+2 exp.
pavonii	2-4 s. teeth+2 l. exp.	4 teeth+2 sp. +2 l. exp.	2 s.+2 l. sp.+2 exp.	disc+4-6 teeth	2 teeth+2 s.+2 l. exp.	4 l. teeth+2 s. exp.	part. disc+2 s. teeth+ 2 exp.	4+2 l. teeth	2 s.+2 teeth
pellans	2 l. exp.	2 teeth+4 exp.	4 sp.+2 l. exp.	disc	2 teeth+4 exp.	4 teeth+2 l. exp.	disc	4 exp.	2 s. teeth+2 l. exp.
persimilis	2 s.+2 l. exp.	4 teeth+4 l. exp.	6 l. exp.	disc+2 exp.	6 exp.	6 exp.	disc	2 teeth+4 s. exp.	4 exp.
persimplex	2 s.+2 l. exp.	4 teeth+4 l. exp.	6 l. exp.	disc+2 exp.	6 exp.	6 exp.	disc+2 exp.	2 teeth+4 s. exp.	4 exp.
peruviensis	2+2 l. exp.	12-14 s. teeth +2 s. exp.	4 teeth+2 exp.	?	?	?	?	?	?
pileini	2 l. exp.	2 teeth+4 exp.	6 exp.	disc+2 exp.	6 exp.	6 exp.	disc+2 s. exp.	2 s. exp.	4 s. exp.
pilosus	0-2 s. teeth+2 l. exp.	10-12 s. teeth +2 s. exp.	4 l. teeth+2 exp.	disc	2 s.+2 l. teeth+4 exp.	4 teeth+2 exp.	disc	2s. +2 l. teeth	2-4 s. teeth
pinelii	2 l. exp.	2 s. teeth+4 exp.	6 exp.	disc+2 exp.	2 s. teeth+2 s.+4 exp.	6 exp.	disc	2 s. teeth	2 s. teeth+4 exp.
placidus	4 s. teeth+4 s. sp.+2 l. exp.	2 teeth+4 l. sp.	2 l. exp.	—	—	—	6 teeth+2 l. exp.	2 s.+2 l. sp.	2 s. exp.
porrasi	2 l. exp.	8 teeth+2 exp.	4 sp.+2 l. exp.	disc+2 s. exp.	2 s. teeth+4 exp.	4 l. teeth+2 l. exp.	disc+2 s. exp.	2 teeth+2 s. exp.	4 teeth+2 l. exp.
prodigiosus	?	?	?	disc+2 exp.	4 s. teeth+4 exp.	2 teeth+4 exp.	disc+2 exp.	2 teeth+2 exp.	2 teeth+4 exp.
pusillus	0-2 s.+2 l. exp.	4 s.+4 l. teeth +2 l. sp.	2-4 teeth+2 exp.	2 l. exp.	2-4 s. teeth+2 l. sp.+2 exp.	2 s. teeth+2 s. exp.	2 l. exp.	4 teeth	4 s. exp.
quadratus	2 l. exp.	10 s. teeth+2 s. exp.	4 sp.+2 exp.	disc	2 s. teeth+4 s. exp.	4 teeth+2 exp.	?	?	?
ramiphilus	2 l. exp.	2-4 s. +4 l. teeth+2 l. exp.	4 sp.+2 exp.	2 l. exp.	4 teeth+4 exp.	4 l. teeth+4 exp.	2 l. exp.	2 teeth+4 s. exp.	4 teeth+2 exp.
resinae	2 l. exp.	2+2 l. sp.	2 teeth+2 sp.+2 s. exp.	—	—	—	?	?	?
robweri	2 l. exp.	6 s. teeth+2 sp.+2 s. exp.	2+2 l. sp.	disc	2 l. teeth+2 exp.	4 teeth	disc	0-2 s. teeth+2 s. exp.	2 s. teeth
scutulatus	2 s.+2 l. exp.	2 teeth+4 l. exp.	4 sp.+2 s. exp.	disc+2 s. exp.	2 teeth+4 l. exp.	2 teeth+4 exp.	disc+2 s. exp.	2 exp.	2 teeth+4 exp.
serraticeps	4 sp.+2 l. exp.	2 s. teeth +6 l. sp.	4 s. teeth+2 exp.	2+2 l. exp.	2 exp.+2 l. sp.	4 s. teeth+2 exp.	4 s. teeth+2 l. exp.	4 s. teeth+2 sp.	2 s. exp.
setulifer	2 l. exp.	10-12 s. teeth +2 s. exp.	4 teeth+2 s. exp.	disc	0-6 s. teeth+4-6 s. exp.	4 teeth+2 s. exp.	disc	2-4 s. teeth+2 s. exp.	2 s. teeth+4 exp.
simillimus	2 s.+2 l. exp.	8 s. teeth+2 l. teeth+4 exp.	4 l. teeth+2 exp.	0	2 s.+2 l. teeth+2 s.+4 exp.	2 teeth+4 exp.	?	?	?
sobrius	2 l. exp.	14 s. teeth+2 s. exp.	2 s.+2 sp.+2 s. exp.	disc+2 s. exp.	6-8 s. teeth+2 exp.	2 teeth+2 sp.+2 s. exp.	disc+2 s. exp.	4 s. teeth+2 exp.	2 s. teeth+4 s. exp.
solidus	2 l. exp.	0-6 s. teeth +2 s. sp.	4 s. teeth+2 exp.	?	?	?	?	?	?
spinosus	4 l. exp.	6 s.+2 l. sp.	2 teeth+2 sp.+2 l. exp.	0-2 s. teeth+2+2 l. exp.	2 s.+4 l. teeth+2 sp.+4 exp.	4 teeth+2 l. exp.	2 l. exp.	2 s.+2 l. teeth	4 exp.

Tab. 7.5. Different morphological adaptations to passive defence in *Cephalotes* female castes. Teeth and spines are interpreted as a defence against vertebrate predation. Expansions of different body parts serve to protect the appendages and should function primarily against other ants and arthropods in general. Species *supercilii* to *† ventriosus*. Abbreviations: l. = large; s. = small, sp. = spines, exp. = expansions.

	Worker			Soldier			Gyne		
	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster	Head	Mesosoma	Pedicel + gaster
supercilii	2 l. exp.	12-14 s. teeth +2 s. exp.	4 teeth+2 exp.	disc+2 exp.	2 s.+2 teeth+4 exp.	2 teeth+4 exp.	disc+2 s. exp.	2 teeth+2 s. exp.	2 s. teeth+4 exp.
taino	2 l. exp.	2+2 l. sp.	2 teeth+2 sp.+2 s. exp.	—	—	—	?	?	?
targionii	0-2 s.+2 l. exp.	18-20 s. teeth + 2 s. exp.	4 teeth+2 exp.	disc+2 exp.	2 s.+2 l. teeth+4 exp.	4 teeth+2 exp.	disc+2 exp.	2 s.+2 teeth+2 s. exp.	2 s.+2 teeth+2 exp.
texanus	2 l. exp.	14 s. teeth+2 s. exp.	4 sp.	disc+2 exp.	4-6 s. teeth+4 exp.	2+2 l. teeth	disc	4 s. exp.	2+2 l. teeth
toltecus	2 l. exp.	6 s. teeth+2 sp.+2 s. exp.	4 sp.	disc	4 teeth+4 exp.	4 l. teeth	?	?	?
trichopborus	2 l. exp.	12-14 s. teeth +2 exp.	2 teeth+4 exp.	?	?	?	?	?	?
umbraculatus	0-2 s. sp.+4 l. exp.	2 s. teeth+4 exp.	6 exp.	disc+0-2 s. teeth+2 l. exp.	0-2 s.+2 l. teeth+2 l. exp.	6 exp.	disc+2 exp.	2 teeth+2 exp.	4 exp.
unimaculatus	2 l. exp.	2+2 l. sp.	2 teeth+2 sp.+2 s. exp.	—	—	—	?	?	?
ustus	2 sp.+2 l. exp.	2 s+4 l. sp. +4 l. exp.	4 sp.+2 l. exp.	4 sp.+2 l. exp.	2 s.+4 l. sp.+4 l. exp.	4 sp.+2 l. exp.	?	?	?
varians	2 l. exp.	0-4 teeth+2-6 s. exp.	0-4 s. to l. teeth+0-6 s. exp.	disc+2 exp.	2 s.+2 teeth+4 exp.	4 teeth+2 exp.	disc+2 exp.	4 teeth	2 exp.
vinosus	2 l. exp.	2+2 l. sp.	2 teeth+2 sp.+2 s. exp.	—	—	—	?	?	?
wheeleri	2 l. exp.	3 s. teeth+2 sp.+2 s. exp.	4 sp.	disc	4 teeth+4 exp.	4 teeth	?	?	?
†alveolatus	2 l. exp.	2 l. exp.	4 s. exp.	?	?	?	?	?	?
†bloosi	2 s.+2 l. exp.	6 s. teeth+2 teeth+2 l. exp.	2 teeth+4 exp.	?	?	?	?	?	?
†brevispineus	2+2 l. exp.	4 s.+2 teeth +2 s.+2 l. exp.	2 teeth+2 exp.	?	?	?	?	?	?
†caribicus	2 s.+2 l. exp.	2 s. teeth+2 s.+2 l. exp.	6 exp.	?	?	?	?	?	?
†dieteri	2 l. exp.	2 s. exp.	4 teeth+2 s. exp.	?	?	?	?	?	?
†bispaniolicus	2+2 l. exp.	2 s.+2 l. exp.	6 exp.	?	?	?	?	?	?
†integerrimus	2 l. exp.	2 exp.	4 teeth+2 exp.	?	?	?	?	?	?
†jansei	2 l. exp.	0-2 s. teeth+2 l. exp.	0-2 s. exp.	?	?	?	?	?	?
†maya	2+2 l. exp.	6 l. exp.	6 l. exp.	?	?	?	?	?	?
†obscurus	2 l. exp.	2-4 s. teeth+2 s.+2 l. exp.	4 teeth+2 s. exp.	?	?	?	?	?	?
†olmecus	2+2 l. exp.	2 teeth+4 l. exp.	6 l. exp.	disc+2 exp.	2 teeth+4 exp.	6 exp.	?	?	?
†poinari	4 l. exp.	2 teeth+4 l. exp.	6 l. exp.	?	?	?	?	?	?
†serratus	2 l. exp.	2 s. to l. exp.	2 exp.	?	?	?	?	?	?
†squamosus	2 s.+2 l. exp.	2 teeth+0-2 s. +2 l. exp.	2 s. teeth+4 exp.	?	?	?	?	?	?
†sucinus	2 s.+2 l. exp.	2 teeth+4 s. exp.	2 teeth+4 exp.	?	?	?	?	?	?
†ventriosus	2+2 l. exp.	2 l. exp.	2 s. teeth+4 exp.	?	?	?	?	?	?

The distribution of the teeth and spines, structures perfectly useless in a confrontation with other ants but with some hindrance power when in contact with an average vertebrate tongue, is slightly different, as one would expect from their presumed function. Cephalic spines of different size and shape are present in 27% of the workers, in 19% of the soldiers and in 27% of the gynes. Mesosomal spines are to be found in 91% of the workers, 89% of the soldiers and 87% of the gynes. It is interesting that workers of few Recent species (*foliaceus*, *patellaris*, *incertus*) are without mesosomal spines compared with the great proportion of fossil ones (7 out of 16). The pedicel bears spines in 84% of the workers, 88% of the soldiers and 67% of the gynes. One pair of mesosomal spines is present in many myrmicine genera but, in *Cephalotes*, the phenomenon is pushed to the known limits for the Formicidae. We explain the greater frequency of spines on ants' mesosoma as compared with other body parts by the practical advantage of carrying spines which don't increase the body size and by the fact that the mesosoma is likely to be the favourite target for small predators.

From the above it appears that lamellae and other body expansions are more common among soldiers, where spines are more developed among workers. This caste-dependant "weaponry" fits the different behaviours of the two castes, with the soldiers remaining essentially in the nest while the workers forage outside. The possession of morphological adaptations to passive defence is regularly reduced among gynes. This might imply either a reduced predation or the possession of other (i. e. chromatic and/or chemical) defence mechanisms. The distribution of the body spines and of the protective body expansions among the two neuter castes for the known species is given in Table 7.

Cephalotes species developed to a much greater degree than other ants an important set of passive defence mechanisms. They encompass the following adaptations: 1) chemical signals of distastefulness, 2) coloration, in which both alternative strategies, i. e. dull (mimetic) or bright (warning) colours have been chosen by different species, 3) morphologic, with the evolution of spines on different body parts and the development of integumental plates under which the appendages are protected.

Every known species shows a different combination of the last two defence mechanisms (chromatic and morphological) and our preliminary GC-MS analyses suggest a comparable diversity of the first (i. e. chemical) as well.

7. Concluding Remarks

BOLTON (1995 a) published a census of the extant ant taxa recognised up to the end of 1993. Comparing the results presented in this paper with the data of BOLTON (l. c.) we see that *Cephalotes* contains 131 described species and, as such, it is the 16th largest ant genus world-wide. Within the Neotropical Region it is, however, the third largest genus (after *Camponotus* and *Pheidole*), but *Cephalotes* (with 113 Neotropical species plus 2 confined to the southern edge of the Nearctic region and 16 amber fossil species) is, together with the equally arboreal *Pseudomyrmex*, (114 Neotropical, 4 Nearctic extant species, and 11 amber fossil species; WARD, 1992) one of the two largest ant genera restricted to virtually only one continent. We believe that the great species richness of *Cephalotes* can be explained by its possessing a unique combination of some of the biological traits described in

Chapter 6, namely polyandry, nesting in pre-existing plant cavities, relying on a virtually unlimited source of food like pollen, multiple adaptations to active (by having a soldier caste and probably by the production of repellent substances) and passive defence, coupled with a probable high rate of spontaneous mutation. Additionally, both the morphologic and chromatic defence strategies described in the previous chapter allow for a large amount of selection-free variation and their intermixture is likely to have contributed significantly to the presently known species diversity.

It appears that at the times of the amber forests in the Caribic and in Mexico, differentiation of and within the genus *Cephalotes* was comparable to the present one.

This diversity of *Cephalotes*, coupled with the demonstration of its minimum age of at least 25–30 million years BP, contrasts with its relatively narrow geographic distribution. 21 of the 24 ant genera containing more than 100 species are distributed over two or more continents. The unusual geographic narrowness of *Cephalotes* could be explained by a younger origin. The fossils described in the present paper show that this presumed young origin must have been at least pre-Miocenic and, to explain both fossil and Recent species richness, this hypothetical young origin should be accompanied by a faster speciation rate compared with those of other ants.

Extinction, in *Cephalotes*, appears nonetheless to be important. In the present paper we recognise 12 extinct Dominican species, as compared with 9 Recent (including two copal) Hispaniolan species, none of which is closely related to the fossil ones. The whole Recent Caribbean fauna (excluding Trinidad which can be considered a piece of S. American mainland) comprises only 12 known species and is poorer than the amber fauna. This situation is not too different from what is known for the genus most comparable to *Cephalotes* with respect to our knowledge of species numbers, distribution, and arboreal habits, i. e. *Pseudomyrmex*. In *Pseudomyrmex* 11 fossil and 6 Recent (including one from copal) species are known from Hispaniola (WARD, 1992). This greater abundance of fossil as compared with the Recent species is a still poorly recognised phenomenon in ants. It probably corresponds, at species level, to the genus-level extinction of the Caribbean fauna already shown by BARONI URBANI (1995). There are currently 43 ant genera known from Dominican amber as compared with 31 genera recorded in the Recent fauna. 21 ant genera appear to have undergone extinction in the Antillean area since amber times. It may be risky to extrapolate additional conclusions from these figures since there are at least two factors which may account for the richness of the fossil record as compared with the extant one:

1) The fossil sample is likely to originate from a broad geological time span. Reviews of the most accurate available age estimates for Dominican amber, in fact, give a minimum and maximum age of 15 to 45 million years respectively (SCHLEE, 1990; POINAR, 1992). During such a time lapse several species successions must have occurred and may easily account for (part of) the species richness recorded in amber *Cephalotes*. ITURRALDE-VINENT & MACPHEE (1996) narrow the age of "all of the *main* amberiferous deposits" (italic ours) to some 15–2 0 million years ago. But their basically sound reasoning is supported largely by incomplete and second hand evidence of palaeontological nature contradicted, e. g., by the cases of dramatic extinctions reviewed and discussed by BARONI URBANI (1995) and by some results of the present paper as already noted in the discussion of the species *squamosus* and *serratus*. None of the 13 fossil Dominican *Cephalotes* has a close relative in the Recent Caribbean fauna.

2) The reduction of the extant species diversity may be explained by simple insularity factors. It is generally assumed that a larger Caribbean landmass existed until the Eocene (KHUDOLEY & MEYERHOFF, 1971). Fragmentation of this landmass probably occurred between the late Eocene and Pliocene while during the Miocene "none of the [Caribbean] islands was large as today's major islands" (KHUDOLEY & MEYERHOFF, 1971: 151).

Either of these two explanations (i. e. fragmentation of a larger landmass and species turnover) could account reasonably well alone for the high extinction rate we are forced to postulate in *Cephalotes*.

There are geological (KHUDOLEY & MEYERHOFF, 1971) and palaeontological (BARONI URBANI, 1980; BARONI URBANI & DE ANDRADE, 1994) reasons for believing that the area where the Dominican amber forest grew was connected to the American mainland at least until the Early Eocene. As one would expect from this hypothesis, its *Cephalotes* fauna is rich, diverse and not too dissimilar from what one would expect to find in a random sample of Recent S. American forest. The relatively high number of Dominican amber species (13) is, in itself, not surprising for a sample of tropical forest: from the Reserva Ducke in Brazil (10,000 ha) 19 *Cephalotes* species have been recorded so far (figure resulting from the data presented in this paper).

Only a few of the most significant synapomorphies we considered can be said to have originated in a fossil species or in its direct ancestor. The two most significant ones are probably those shared by the Mexican fossils of the *grandinosus* clade, the rugulation on the extensor face of the worker tibiae and the carinate hind femora of the soldiers, two synapomorphic traits characterising the small subclade (†*olmecus*, (†*maya*, *foliaceus*)).

A character shared by all fossil species is the visible scapular angle of the workers. Since in our phylogeny this trait results to have appeared 10 times independently in *Cephalotes* evolutionary history we regard this fact as a simple curiosity.

From our results it appears that the study of the fossils improved only slightly our understanding of the Recent species but knowledge of the Recent species is essential to the comprehension of the fossils. It is certainly so, but for purely numerical reasons: the fossils described in this paper represent only 12% of the known *Cephalotes* species. If this proportion was reversed, the conclusion would also be reversed. In the case of *Cephalotes*, however, a study of the fossil species only slightly beyond their formal description would have been destined to major failures without considering their Recent relatives.

According to our phylogenetic reconstruction of Fig. 24, the Hispaniolan endemic *hamulus* clade is the one containing all the less specialised species of the genus. Members of this clade – comprising eight known species – are likely to represent not only the most characteristic speciation event of the Hispaniolan ant fauna as a whole, but also the primitive *Cephalotes* population of the island. Only one more species of *Cephalotes* is known from the extant Hispaniolan fauna (*C. decoloratus*, equally endemic and belonging to an unrelated clade for which fossils are also unknown). The 12 Recent Caribbean *Cephalotes* species all belong to clades very distant from the Hispaniolan *hamulus* clade. These Hispaniolan endemics never acquired important evolutionary traits present in most other *Cephalotes*, like the soldier caste, the hypostomal sulci, etc. This lack of specialisation of the extant Hispaniolan fauna contrasts sharply with the fact that all Hispaniolan fossils are more specialised than their Recent sympatric but allochronic relatives. All the

Dominican fossil species, morphologically, could be mistaken for Recent mainland species. Only one of these fossils (*C. brevispineus*) belongs – together with other Recent S. American species – to a relatively early differentiated clade.

The fact that all plesiomorphic species of *Cephalotes* are known from the Recent Hispaniolan fauna and not from the fossil record could be explained as a case of tardy insular explosive speciation. This oddity is further emphasised by the fact that both known Dominican copal species also belong to the *hamulus* clade. The age of the copal species is likely to be much younger than that of the amber fossils, and closer to, or coincident with, that of the extant fauna: a sample of Dominican copal from Cotuí, analysed by means of the ^{14}C method, was less than 280 years old (reference year 1950; SCHLEE, 1984).

To explain the complete dissimilarity between the fossil and the Recent Hispaniolan *Cephalotes*, with the plesiomorphic species in the Recent fauna and the apomorphic ones in the fossil fauna, we suppose that representatives of the *hamulus* clade are absent in the fossil record since they were as rare at the times of the amber forest (25–40 million years ago) as they are today. We assume furthermore that fragmentation of the Eocenic Hispaniolan land mass drove the original amber forest fauna to extinction with the exception of an ancestral member of the *hamulus* clade. Circumstantial evidence for the local extinction of *Cephalotes* species as a consequence of area reduction has been given above. The ancestral species of the *hamulus* clade, of which we have no fossil record, must have undergone multiple speciation due to the occupation of fragmented niches resulting from continuing vulcanism (a phenomenon outlined by KHUDOLEY & MEYERHOFF, l. c.). If this is true, species differentiation in the Hispaniolan *hamulus* clade may have been favoured by lack of competition with other members of the genus. And speciation probably occurred much later than for most other species of the genus, after the late Miocene or early Pliocene, a hypothesis matching the presumed palaeogeography of the Caribic with the remarkable morphological uniformity among all members of the clade.

We have already said that the Dominican amber *Cephalotes* fauna could be mistaken for a random sample taken from a Recent Neotropical forest. The same is true for the three Mexican amber species which, phylogenetically, are not separate in any significant way from the Dominican fossils. We have examples of Dominican fossils which, according to our phylogenetic reconstruction, belong to clades differentiated earlier and later than those containing the Mexican fossil species.

The significance of the four Mexican amber *Cephalotes* is rather different from the picture suggested by the single Mexican fossil ant known so far (*Aphaenogaster praerelicta*) and described by DE ANDRADE (1995). This species shows unequivocal relationships with a Recent Hispaniolan one.

One of the Mexican fossils (*poinari*) appears to be the basal-most species of the *biguttatus* clade which contains six species, two of which are from Dominican amber. The remaining two Mexican fossil species (*olmecus* and *maya*), however, are the sole fossil members of a small clade containing only three species. The single extant member of this clade, *foliaceus*, is remarkable for showing to the greatest extent the two most obvious *Cephalotes* adaptations: flattening of the entire body and growth of lateral expansions. Both Mexican fossils share with *foliaceus* an extremely flat body and enormous lateral expansions, a fact suggesting that the unconstrained increase in these passive defence mechanisms may be not a very rewarding option.

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10. Index of Latin names

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